

## Chapter 12

# Introgression and Exploitation of Biotic Stress Tolerance from Related Wild Species in Wheat Cultivars

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**Abstract** Bread wheat is one of the three most important cereal crops which has major role in feeding the population globally. Biotic stresses, mainly the fungal diseases, pose major constraint to wheat production. To combat against these diseases, continuous efforts have been made to mine genes from wide variety of sources including primary, secondary, and tertiary gene pools of cultivated wheat which are rich sources of genes against different biotic stresses. More than 100 resistance genes against leaf rust, stripe rust, stem rust, and powdery mildew have been identified from these gene pools and successfully transferred to cultivated wheat. The transfers from primary gene pool are achieved through homologous pairing while transfer from secondary and tertiary gene pool requires special chromosome engineering techniques for affecting transfers through induced homoeologous pairing or translocations. The introgressions have been reported as small cryptic alien segments or complete chromosome arms or chromosomes such as chromosome addition and substitution lines. Molecular cytogenetic techniques such as genomic in situ hybridization (GISH) have proved to be a highly efficient technique to directly and precisely detect the alien segments in wheat while molecular marker technologies now combined with next-generation sequencing techniques have facilitated the mapping as well as marker-based mobilization of alien genes to cultivated wheat background. Present review gives a brief description of the contributions of different gene pools of wheat toward the biotic stress resistance, methodologies of gene transfer, characterization of these transfers, and use of the molecular marker technologies for precisely mapping the alien genes for resistance to various biotic stresses in wheat.

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## 12.1 Introduction

Wheat is one of the most important staple foods of the world, occupying 17 % of the total crop acreage worldwide, feeding nearly half of the world population. A steadily growing population and limited areas available for growing crops make it necessary to secure and extend yield potential. Exploitation of the basic genetic principles has resulted in the development of high-yielding varieties and this productivity is maintaining its rate of progress. Genetic manipulation of dwarfing genes coupled with improved production technology led to the green revolution during the mid-1960s. This led to quantum jump in yield of two major cereals: wheat and rice. Since then increase in yield has been consistent but slow. Global population has doubled during last 45 years and expected to reach 9 billion by 2050. Feeding a population of 9 billion people would require raising overall food production by 70 %. Production in the developing countries would need to be almost double. Quantity of food produced per capita has been declining for last more than 20 years estimated based on available cereal grains, which make up about 80 % of the world's food supply. The present rate of increase in the production of three major cereals may not keep pace with the growing world population.

The population of India will be 1.4 billion by 2020 and will need ~ 109 million tons (MT) of wheat to meet its food demands. Wheat production in India has shown an upward trend for the last five years producing a record of 95.91 MT during 2013–2014 harvest (<http://agricoop.nic.in/imagedefault/trade/wheatnew.pdf>). However, most of the existing wheat varieties, which were released more than a decade ago, are showing signs of fatigue and have succumbed to the new races of the stripe rust. The future techniques will require newer wheat-breeding strategies including quicker and reliable selection methods to have designer plants combining high yield and disease resistance. Breeding for resistance against diseases is an important objective of wheat-breeding programs globally. It is also widely recognized that in the absence of diverse genetic input, the breeding approach may not prove fruitful. The genetic variability for resistance to major diseases, viz., yellow rust, leaf rust, stem rust, Karnal bunt, powdery mildew and leaf blight within bread wheat germplasm needs to be supplemented with identification and mobilization of new genes from untapped germplasm collections. Wild relatives of wheat provide a rich reservoir of genes for resistance to various wheat diseases and can provide a valuable source of genetic variation for the improvement of biotic stress tolerance in cultivated wheat (Sharma and Gill 1983; Jiang et al. 1994; Friebe et al. 1996; Singh et al. 1998). A thorough knowledge of phylogenetic relationships of cultivated wheats with its wild progenitors and related species is absolutely essential for the successful introgression and exploitation of useful variability in the wheat germplasm.

## 12.2 Major Diseases of Wheat

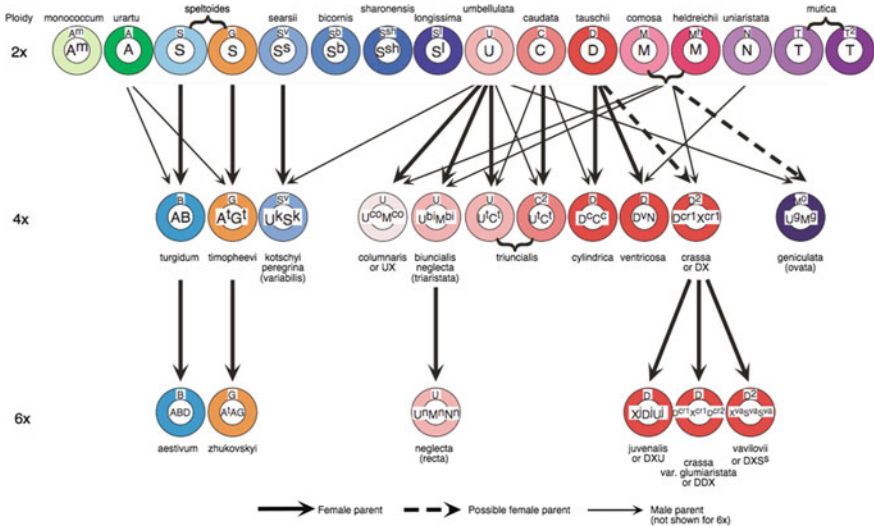
The rust diseases of wheat have historically been one of the major productivity constraints for wheat cultivation globally. Stem (or black) rust caused by *Puccinia graminis* is one of the most significant threats to global wheat production (Singh et al. 2008) with the emergence of Ug99 group of stem rust races. Leaf rust caused by *Puccinia triticina* and stripe rust caused by *Puccinia striiformis* continue to pose a major threat to wheat production over a large area. Leaf rust and stripe rust could affect production on approximately 60 (63 %) and 43 (46 %) m ha, respectively, in Asia, if susceptible cultivars were grown there (Singh et al. 2004a). Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is another important foliar disease of wheat occurring worldwide. It competes for nutrients and reduces the photosynthetic capacity of the leaves. Severe epidemics of this disease often occur in areas with cool and humid climates, causing significant yield losses (Bennett 1984). Breeding and deployment of powdery mildew resistant cultivars is the economical and environmentally friendly method to avoid fungicide applications and reduction in the yield due to diseases. The discovery and utilization of new powdery mildew-resistant genes has been a long-term objective for wheat geneticists and breeders worldwide.

Karnal bunt (KB) of wheat, caused by *Tilletia indica*, was first reported in Karnal, India (Mitra 1931). The disease was soon detected in numerous other regions throughout Northern and Central India. Later, the disease was found to occur in several other countries such as Nepal, Pakistan, Afghanistan, Iran, Iraq, South Africa, Mexico, and USA (Rush et al. 2005). Wheat grains infected by *T. indica* produce trimethylamine and flour from grains with over 3 % bunted kernels imparts an off-color and unpleasant odour (Mehdi et al. 1973). The disease has become important worldwide due to the strict international quarantine measures imposed by a number of countries (Rush et al. 2005). The pathogen is soil, seed, and airborne in nature and hence difficult to control once introduced and established in an area. The host genetic resistance is the most effective, economical, and eco-friendly method of KB management. However, development of KB resistant varieties is difficult due to limited variability for KB resistance in hexaploid wheat (Dhaliwal et al. 1993), quantitative nature of inheritance, and considerable influence of environment on screening for disease resistance (Dhaliwal and Singh 1997). Also, our knowledge of genetics of this host–pathogen system is limited. Inheritance studies have indicated that KB resistance is governed by two or more genes which act additively (Morgunov et al. 1994; Fuentes-Davila et al. 1995; Singh et al. 1995; Villareal et al. 1995; Singh et al. 1999).

### 12.3 Phylogeny of Polyploid Wheats

Hexaploid wheat originated in two steps of natural hybridization and chromosome doubling, thus comprising genomes of three diploid species (Fig. 12.1). One wild diploid *Triticum* species and two species of the closely related genus *Aegilops* are the wild progenitors of bread wheat. Kihara (1919) and Sax (1922) based on the cytological data on chromosome pairing in interspecific hybrids among species of different ploidy levels indicated that *T. monococcum* and *T. turgidum* have one genome in common while *T. turgidum* and *T. aestivum* share two genomes in common. A diploid wheat species *T. urartu* was found to be a distinct biological species, reproductively isolated from *T. monococcum* (Johnson and Dhaliwal 1976) and on the basis of molecular data it was found that *T. urartu* and not *T. monococcum* contributed the A genome to polyploid wheats (Dvorak et al. 1993). There has been a lot of controversy regarding *Ae. speltoides* as the donor of the B and G genomes to polyploid wheats (Sarkar and Stebbins 1956; Riley et al. 1958). Evidences from diverse sources indicate that *Ae. speltoides* contributed the G genome to *timopheevii* wheats, whereas *Ae. speltoides* with a different cytotype or a species closely related to it contributed the B genome to *turgidum* wheats (Jiang and Gill 1994).

McFaden and Sears (1946) and Kihara (1944) unequivocally demonstrated that *Ae. tauschii* was the D genome donor of bread wheat which arose from a hybridization between *T. turgidum* and *Ae. tauschii* var. *strangulata* about 7000 years ago (Dvorak et al. 1998). The tetraploid parent probably was cultivated emmer, ssp. *dicoccum* because the range of wild progenitor, ssp. *dicoccoides* does not overlap with that of *Ae. tauschii*. Vast cytological, molecular cytogenetic, and



**Fig. 12.1** Phylogeny of *Triticum* and *Aegilops* species (Source BS Gill, Wheat Genetic and Genomic Resource Centre)

molecular mapping data in Triticeae and related tribes indicate that a very high level of gene content and synteny is maintained among different species thus making it possible to substitute complete chromosome or chromosome segment carrying useful traits from progenitor and non-progenitor genomes into any of the wheat A, B, and D genomes without drastic effects. The ease of transfer of useful variability and its subsequent commercial exploitation would, however, depend on the evolutionary relationship and differentiation between the donor and the recipient genomes.

## 12.4 Gene Pools of Wheat

The most recent taxonomic status of *Triticum* and *Aegilops* genera to which the cultivated wheats and their progenitors belong as established by van Slageren (1994) is given in Table 12.1 with some modifications. There are three ploidy levels in both the genera with  $2n$  chromosomes 14, 28, 42 and the basic chromosome  $x = 7$  in all the species. Other genera of Poaceae such as *Secale*, *Hordeum*, *Dasopyrum*, *Agropyron*, *Elymus*, *Leymus*, *Elytrigia*, and *Thinopyrum* are also important for introgression of useful variability into cultivated wheats.

On the basis of their genomic constitution, the wild relatives of wheat can be classified into primary, secondary, and tertiary gene pools (Jiang et al. 1994; Friebe et al. 1996). Species belonging to the primary gene pool share homologous genomes with cultivated wheat (Fig. 12.2). This group includes land races of *T. aestivum*, the wild and cultivated forms of *T. turgidum*, and donor species of the A and D genomes of bread wheat, *T. monococcum*, *T. urartu*, *T. boeoticum*, and *Ae. tauschii*. Gene transfer from these species can be achieved by direct hybridization, backcrossing, and selection (Friebe et al. 1996). No special cytogenetic manipulation except embryo rescue in certain cases is necessary to produce  $F_1$  hybrid (Jiang et al. 1994). Many genes conferring resistance to diseases and insect pests have been transferred using this method and several of them are still being exploited in cultivar improvement (McIntosh et al. 1995a, b).

The secondary gene pool of common wheat includes the polyploid *Triticum* and *Aegilops* species that have at least one genome in common with wheat. Gene transfer from these species by homologous recombination is possible, if the target gene is located on a homologous chromosome. However, if the genes are present in a non-homologous genome, special cytogenetic manipulations are required. These species have contributed several resistance genes that are being used in cultivar development (Jiang et al. 1994).

Species belonging to the tertiary gene pool are more distantly related. Their chromosomes are not homologous to those of wheat. Gene transfer from these species cannot be achieved by homologous recombination, chromosome pairing, and recombination between wheat chromosome and alien chromosomes (Jiang et al. 1994; Friebe et al. 1996). Special cytogenetic techniques are required to ensure compensating transfers with least linkage drag for commercial exploitation of

**Table 12.1** Species of genus *Triticum* and *Aegilops* and their genomic constitution

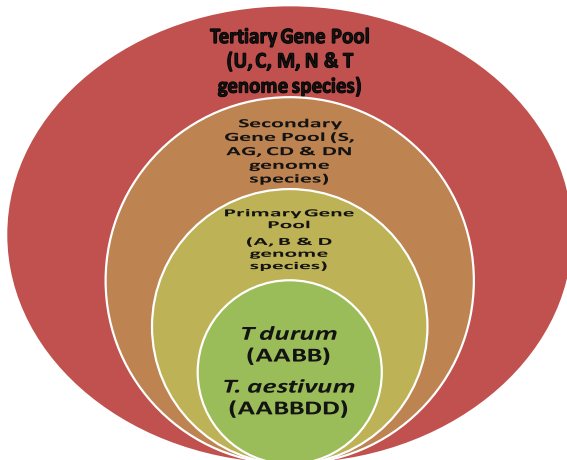
Species	Genome	Synonyms
<i>Triticum</i>		
<b>Diploids</b>		
<i>T.monococcum</i> L. (Einkorn)	$A^m$	<i>T. boeoticum</i>
var. <i>boeoticum</i>		<i>T. aegilopoides</i>
var. <i>aegilopoides</i> (wild)		
<i>T. urartu</i> Tumanian ex Gandilyan(wild)	A	
<b>Tetraploids</b>		
<i>T. turgidum</i> L.	AB	<i>T. durum</i>
var <i>durum</i> , (macaroni wheat)		
var. <i>dicoccum</i> (emmer wheat)		<i>T. dicoccum</i>
var. <i>polonicum</i> (polish wheat)		<i>T. polonicum</i>
var. <i>carthlicum</i> (persian wheat)		<i>T. carthlicum</i>
var. <i>dicoccoides</i> (wild emmer)		<i>T. dicoccoides</i>
<i>T. timopheevii</i> (cultivated)	$A^1G$	<i>T. araraticum</i>
var. <i>araraticum</i> (wild <i>timopheevi</i> )		
<b>Hexaploids</b>		
<i>T. aestivum</i> (common or bread wheat)	ABD	<i>T. vulgare</i>
var. <i>spelta</i> (spelta or dinkel wheat)		<i>T. spelta</i>
var. <i>compactum</i> (club wheat)		<i>T. compactum</i>
var. <i>sphaerococcum</i> (Indian dwarf wheat)		<i>T. sphaerococcum</i>
var. <i>vavilovii</i>		<i>T. vavilovii</i>
var. <i>macha</i>		<i>T. macha</i>
<i>T. zhukouskyi</i>	$A^1A^mG$	
<i>Aegilops</i>		
<b>Diploid</b>		
<i>Ae. speltooides</i> Tausch	S	<i>T. speltooides</i> var. <i>aucheri</i> Var. <i>ligustica</i>
<i>Ae. longissima</i> Schweinfx Maschl	$S^l$	<i>T. longissimum</i>
<i>Ae. sharonensis</i> Eig	$S^{sh}$	<i>T. sharonense</i>
<i>Ae.searsei</i> Feldman & Kislv ex Hammmer	$S^s$	<i>T. searsii</i>
<i>Ae. bicornis</i> (Forsk) Jaub & spach	$S^s$	<i>T. bicornis</i>
<i>Ae. tauschii</i> (Coss) Schmalh	D	<i>T. tauschii</i> var. <i>strangulata</i> var. <i>tauschii</i>
<i>Ae. mutica</i> Boiss	T	<i>T. tripsacoides</i>
<i>Ae. comosa</i> (Sm.& Sibth)Richter	M	<i>Ae. heldreiohii</i> , <i>T. comosum</i>
<i>Ae. caudata</i> L.	C	<i>Ae. markgrafii</i> , <i>T. dichasian</i>
<i>Ae. umbellulata</i> Zhuk	U	<i>T. umbellulatum</i>
<i>Ae. uniaristata</i> Vis	N	<i>T. uniaristatum</i>

(continued)

**Table 12.1** (continued)

Species	Genome	Synonyms
<b>Tetraploid</b>		
<i>Ae. cylindrica</i> host	$D^cC^c$	<i>T. cylindricum</i>
<i>Ae. ventricosa</i> Tausch	$D^VN^V$	<i>T. ventricosum</i>
<i>Ae. crassa</i> L.	$D^{CL}M^c$	<i>T. crissum</i>
<i>Ae. triuncialis</i> L.	$UC^t$	<i>T. triunciale</i>
<i>Ae. geniculata</i> Roth	$UM^o$	<i>T. ovatum</i>
<i>Ae. neglecta</i>	$UM$	<i>Ae. triaristata</i>
<i>Ae. columnaris</i> Zhuk	$UM$	<i>T. columnare</i>
<i>Ae. biuncialis</i> Vis	$UM$	<i>Ae. lorentii</i> , <i>T. machrochaetum</i>
<i>Ae. kotschyi</i> Boiss	$US^t$	<i>T. kotschyi</i>
<i>Ae. peregrina</i>	$US^t$	<i>Ae. variabilis</i>
<b>Hexaploids</b>		
<i>Ae. juvenalis</i> (Thell) eig	$DMU$	<i>T. juvenile</i>
<i>Ae. vavilovii</i> (Zhuk) Chennav	$DMS$	<i>T. syriacum</i>
<i>Ae. crassa</i> var. <i>glumiaristata</i>	$DDM$	<i>T. crassum</i> (6x)
<i>Ae. neglecta</i> var. <i>recta</i>	$UMN$	<i>Ae. triaristata</i> (6x)

**Fig. 12.2** Gene pools of wheat



introgressed derivatives. Even though such transfers may include an entire chromosome arm or part of an arm, these have been successfully bred into commercial wheat cultivars because the alien chromosome arm or segment genetically compensates for the missing wheat chromatin.

Though gene transfers from distant relatives is more difficult, but it has been established that the more distant from wheat the relative is, the more likely it is to have genes that are not present in any of the wheat cultivars themselves. Some of the genes may be of great value to wheat growers (Sears 1981).

## 12.5 Steps and Techniques for Alien Gene Introgression

Various steps for successful hybridization, introgression of useful variability, and characterization of introgressed derivatives are listed below:

### 12.5.1 Steps of Introgression

- i. Synchronization of flowering
- ii. Embryo rescue
- iii. Overcoming hybrid dysgenesis
- iv. Synthetic amphiploid
  - v. Circumventing gene suppression
  - vi. Development of alien addition and homoeologous substitutions
  - vii. Induction of homoeologous pairing and translocations

Introgression of useful variability from related cultivars and wild species into cultivated bread and durum wheats has been reviewed by Cox (1998). In this chapter, we will describe only the techniques for promoting alien gene transfer and characterization of interspecific derivatives.

### 12.5.2 Techniques for Promoting Alien Gene Transfer

#### 12.5.2.1 Induced Homoeologous Pairing

The pairing affinity among homoeologous chromosomes of the three wheat genomes is suppressed by the genetic activity of the pairing homoeologous gene, *Ph1*, on the long arm of chromosome 5B. In the presence of *Ph1*, the alien chromosomes will not pair with their wheat homoeologues. Therefore, different strategies for promoting pairing between wheat and alien chromosomes must be used.

#### 12.5.2.2 Use of 5B—Deficient Stocks

If an alien species can be crossed directly with bread wheat, plants monosomic for chromosome 5B can be used as female parents in crosses with it. About 75 % of the offspring will be deficient for 5B. Progeny lacking 5B will show considerable homoeologous pairing and desired recombinants may be recovered by backcrossing them with the wheat parent.



### 12.5.2.3 Crosses with Species Carrying a Suppressor of *Ph1*

An effective method of inducing homoeologous pairing is by crossing wheat with certain genotypes of alien species that inactivate the homoeologous pairing suppressors. *Aegilops speltoides*, for example, is known to suppress the activity of *Ph1* in hybrids with wheat, resulting in high homoeologous pairing (Riley 1960). These hybrids are then backcrossed to wheat and direct transfer of genetic material from *Ae. speltoides* to wheat may be obtained. Riley et al. (1968a) used this technique to transfer stripe rust resistance from *Ae. comosa* (MM) to wheat. Chen et al. (1994) transferred a dominant homoeologous pairing inducer *Ph<sup>1</sup>* gene from *Ae. speltoides* into hexaploid wheat cultivar Chinese Spring (CS). Aghaee-Sarbarzeh (2000) has successfully induced homoeologous pairing between alien chromosomes and their wheat homoeologues using Chinese Spring stock with suppressor for *Ph* locus. The availability of this system in *T. aestivum* would allow the exploitation of this system for reducing the linkage drag during the transfer of alien genes.

### 12.5.2.4 Crosses Involving *Ph* Mutants

A high-pairing mutation involving a small, intercalary deficiency for *Ph1* was produced by Sears (1977) and is designated *ph1b*. Subsequently, another mutation (a terminal deficiency) that conditions an intermediate level of homoeologous pairing was induced. This mutant is designated as *ph2a* and is located on the short arm of 3D. It seems that the level of homoeologous pairing obtained in the absence of *Ph1* is about the highest obtainable. Another mutant induced in the durum wheat cultivar Cappelli has been designated *ph1c* and is being used in promoting homoeologous pairing in intergeneric hybrids. These mutants, when crossed with alien species, may induce wheat–alien chromosome pairing and thus facilitate desired gene transfer into wheat.

### 12.5.2.5 Chemical Agents

Knight et al. (2010) showed in detached wheat tillers of wheat–rye hybrids that okadaic acid (OA), a drug known to induce chromosome condensation, can be introduced into wheat interspecific hybrids prior to meiosis to induce homoeologous chromosome pairing. This pairing occurs in the presence of the *Ph1* locus, which usually suppresses pairing of related chromosomes through delayed condensation. The timing of chromosome condensation during the onset of meiosis is an important factor in controlling chromosome pairing. This indicated that with the correct concentration of OA, chromosome pairing can be induced in wheat–rye interspecific hybrid plants even in the presence of the *Ph1* locus, mimicking the pairing observed in the absence of *Ph1*. Thus, this approach of treating detached wheat tillers with a drug can in principal provide a powerful method to enhance genetic exchange between chromosomes once standardized for in vivo system.

### 12.5.2.6 Radiation-Induced Translocations

Sears (1956) pioneered a method using ionizing radiation to produce translocation between homoeologous chromosomes. He developed synthetic amphiploids by crossing *Ae. umbellulata* (UU) with *T. dicoccoides* (AABB) which was further crossed with Chinese Spring wheat to transfer leaf rust resistance from *Ae. umbellulata* to bread wheat. After two backcrosses of the F<sub>1</sub> plants (pollen parent) to Chinese Spring leaf rust-resistant plants with 21 bivalents plus an added *Ae. umbellulata* (UU) chromosome were obtained, including one carrying an isochromosome for the long arm of the *umbellulata* chromosome, the arm carries the resistance gene. Plants carrying the isochromosome were irradiated with X-rays when the first spikes were entering meiosis. Pollen from these plants was used to pollinate Chinese Spring. Since the U chromosome was deleterious and showed low transmission through the pollen, it was expected that most resistant progeny would carry a translocation. Of the 6091 plants, 132 were rust-resistant and 40 proved to carry translocation. One line was named Transfer and its gene for resistance, *Lr9*, was used in several cultivars in the USA.

### 12.5.2.7 Spontaneous Translocations

During meiosis in wide crosses, chromosomes often occur as univalents which may divide incorrectly to give rise to telocentrics; reunions are known to occur between different telocentrics resulting in novel chromosomes with desired genes. Based on this phenomenon, Sears (1972) proposed a method of transferring genes involving the exchange of whole chromosome arms. In a wheat–alien hybrid having wheat as well as an alien monosome, both univalents may occasionally divide incorrectly in the same sporocyte and thus a wheat chromosome arm may rejoin an alien chromosome arm. Although, frequency of such unions is low, Zeller (1973) could produce two wheat–rye exchanges in crosses between Chinese Spring monosomics and Chinese Spring–Rye addition lines. Several European cultivars carry a spontaneous translocation between chromosome 1B of wheat and 1R of rye. The Veery lines developed in the CIMMYT program in Mexico also carry a 1BL/1RS translocation derived from the winter wheat, Kavkaz. They have proven to be very high yielding as well as having good resistance to several diseases.

### 12.5.2.8 Introgression via Direct Hybrid

Gene transfer by direct backcrossing is possible in those combinations where there are one or more genomes homologous between recipient and donor species (Table 12.2). Hybrids between durum or common wheat and related donor species are generally male sterile which set seed when backcrossed. Gerechter-Amitai and

**Table 12.2** Gene transfer into wheat by direct backcrossing

Recipient parent	Donor parent	Trait	References
<i>T. durum</i>	<i>T. boeoticum</i>	Stem rust	Gerechter-Amitai et al. (1971)
<i>T. aestivum</i>	<i>Ae. speltoides</i>	Leaf rust	Dvorak (1977)
<i>T. aestivum</i>	<i>T. monococcum</i>	Leaf rust	Cox et al. (1994)
<i>T. aestivum</i>	<i>Ae. squarrosa</i>	Leaf rust	Cox et al. (1994)
<i>T. durum</i>	<i>T. monococcum</i>	Hessian fly	Cox and Hatchett (1994)
		Herbicide tolerance	Gill et al. (1987)
<i>T. durum</i>	<i>T. timopheevii</i>	Glume blotch	Ma et al. (1995)
		Stem rust	
		Powdery mildew	
<i>T. aestivum</i>	<i>T. araraticum</i>	Powdery mildew	Dhaliwal et al. (2002)
		Stripe rust	
		Leaf rust	
<i>T. aestivum</i>	<i>Ae. triuncialis</i>	Leaf rust, powdery mildew	Harjit Singh et al. (2000)
		Cereal cyst nematode	
<i>T. aestivum</i>	<i>Ae. ovata</i>	Leaf rust, stripe rust	Dhaliwal et al. (2002)

Gramma (1974) transferred stem rust-resistant gene from *T. monococcum* spp. *aegilopoides* into *T. durum* by simple backcrossing. Sterile triploid hybrid ( $A^mAB$ ) produces viable female gamete with only 14 chromosomes ( $A^m/AB$ ) and on backcrossing with recurrent durum parents as male, fertile durum derivatives are recovered in  $BC_1$  generation with complete recovery of B genome and recombination and assortment of  $A^m/A$ . During gene transfer via direct hybrids, embryos have to be rescued in wider ploidy level differences between the recipient and the donor species such as between *T. aestivum* and *Ae. tauschii* or *T. monococcum*. Moreover, there is very little seed set on backcrossing the sterile  $F_1$  hybrids as the chances of formation of viable female gametes are very rare unless and until there is unreduced gamete formation in certain combinations. It is desirable in certain cases with partial male fertility to use early backcross generation derivatives as male parent for rapid recovery of euploid and elimination of unwanted chromosomes and translocations. Repeated backcrossing and selfing of recovered euploid with alien introgression accompanied with stringent selection may be required for rapid recovery of cultivated background without any linkage drag. At PAU, we have successfully transferred genes for disease resistance and HMW glutenin subunits from several *Triticum* and *Aegilops* species into wheat and durum cultivars via direct hybridization and backcrossing.

### 12.5.2.9 Gene Transfer via Synthetic Amphiploids

Synthetic amphiploids, being fertile and true breeding, have been used for transfer of genes for disease resistance from diploid to tetraploid or hexaploid wheat (Table 12.3). In majority of cases of gene transfer from diploid species via synthetic amphiploids, *T. durum* has been used as one of the buffering or bridging species for making synthetic amphiploids for their ultimate hybridization with bread wheat cultivars. During development of synthetic amphiploid between *T. durum* and the donor diploid species such as *T. monococcum*, *Ae. umbellulata*, *Ae. caudata*, doubling of chromosomes of sterile triploid hybrids is required, whereas no colchicine treatment is needed in *T. durum* × *Ae. tauschii* and *T. durum* × *Ae. longissima* hybrids as there is a high degree of seed set on selfing due to unreduced female and male gamete formation. It is, however, very important to use *T. durum* parent susceptible to a particular disease or with low expression of a trait that is intended to be transferred from a particular diploid species so that concomitant transfer for the same trait for *T. durum* parent does not get confounded or interfere with the monitoring of genes transferred from the diploid donor species.

Series of *durum*–*Ae. tauschii* synthetic amphiploids have been developed and very extensively used at CIMMYT, Mexico, for transfer of disease and insect resistance and quality traits from *Ae. tauschii* into bread wheat. The suppression of disease resistance in certain amphiploids due to the presence of gene suppressors in *T. durum* and *T. aestivum* has to be avoided through careful selection of *T. durum* and *T. aestivum* parents. Due to the presence of *Ne1* gene in most of the *T. durum* cultivars and *Ne2* in most of the CIMMYT-derived *T. aestivum* lines, hybrids between wheat and synthetic *durum*–*tauschii* often end up with hybrid necrosis. To avoid hybrid necrosis, we have developed a WL711 version without *Ne* alleles, which is being exhaustively used for gene transfer. In case of intended gene transfer from a non-progenitor species with non-homologous genome, it will be desirable to

**Table 12.3** Gene transfer into common wheat via synthetic amphiploids

Amphiploid	Trait	References
<i>Ae. speltoides</i> – <i>T. monococcum</i>	Leaf rust	Kerber and Dyck (1990)
	Stem rust	
<i>T. durum</i> – <i>T. monococcum</i>	Leaf rust	Valkoun et al. (1986)
	Stripe rust	
	Karnal bunt	Kuraparthi et al. (2001) Dhaliwal et al. (2002)
Tetra Canthatch– <i>Ae. tauschii</i>	Leaf rust	Kerber and Dyck (1969)
<i>T. durum</i> – <i>Ae. tauschii</i>	Septorial leaf blotch	May and Lagudah (1992)
	Karnal bunt	Villareal et al. (1994a,b)
<i>T. durum</i> – <i>Ae. umbellulata</i> / <i>T. aestivum</i>	Leaf rust	Chhuneja et al. (2008b)
	Stripe rust	

cross the amphiploid with *Ph<sup>1</sup>* stock for inducing homoeologous pairing before backcrossing with the elite wheat variety.

Polyploid wheats have been successfully hybridized with several distantly related species and genera of Poaceae including *Aegilops*, *Agropyron*, *Leymus*, *Elymus*, *Secale*, *Hordeum*, *Haynaldia*, *Thinopyrum*, *Sorghum*, *Pennisetum*, and *Zea mays* due to their higher ploidy levels, buffering genomes, and genes controlling crossability which has been extensively reviewed (Sharma and Gill 1983; Jiang et al. 1994).

## 12.6 Molecular Cytogenetic Characterization of Alien Introgressions

Characterization of a wheat–alien chromosome translocation includes the identification of the translocated chromosome, localization of the break points, and estimation of the amount of the transferred alien chromatin. Molecular cytogenetic techniques such as genomic in situ hybridization (GISH) have proved to be the most efficient techniques to directly and precisely detect the alien segments in wheat. It allows rapid identification of individual chromosomes in situ (on a glass slide). Non-isotopic methods of mapping DNA sequences in situ on chromosomes on a glass slide were used to construct a molecular karyotype of wheat (Rayburn and Gill 1985). These molecular cytogenetic methods of genome analysis have greatly facilitated cytogenetic analysis in wheat and related species, especially the analysis of alien transfers (Friebe et al. 1991, 1996).

A number of wheat–alien translocations conferring resistances to diseases and pests have been successfully characterized (Table 12.4) through strenuous and collaborative efforts at the international level, some of which have been included in an excellent review by Friebe et al. (1996). Eleven of the 58 wheat–alien translocations analyzed by C-banding and GISH were whole arm translocations with break points within the centromere, whereas 45 translocations were terminal. There were only two intercalary translocations with an alien segment inserted into wheat chromosome arm. The majority of the translocations obtained through irradiation were of non-compensating type involving transfers between non-homoeologous chromosome arms, whereas most of the wheat–alien translocations produced by induced homoeologous recombinations were of compensating type with greater agronomic potential.

In situ hybridization was initially developed, independently, by Gall and Pardue (1969) and John et al. (1969). Genomic in situ hybridization (Pinkel et al. 1986) is a special type of fluorescence in situ hybridization, which uses genomic DNA of donor species as a probe in combination with an excess amount of unlabeled blocking DNA, to monitor alien chromatin introgressions. Genomics in situ hybridization using genomic DNA of the donor species as probe offers advantages as compared to other methods as it leads to the ‘painting’ of all alien chromatin

**Table 12.4** Characterization of wheat-alien translocations

S.No	Alien species	Alien target genes	Description	Mode of transfer	Type*	Germplasm
1	<i>Ae. umbellulata</i>	<i>Lr9<sup>a</sup></i>	T6BS.6BL-6U#1L	Irradiation	C	Transfer T47
2	<i>Ae. umbellulata</i>	<i>Lr9</i>	T4BL.4BS-6U#1L	Irradiation	N	T41
3	<i>Ae. speltoides</i>	<i>Lr28<sup>a</sup></i>	T4AS.4AL-7S#2S	Homoeol. rec.	C	2A/2 M#4/2
4	<i>Ae. speltoides</i>	<i>Lr32</i>	T2DL-2S#1L.2S#1S	Homoeol. rec.	C	C82.2
5	<i>Ae. speltoides</i>	<i>Lr35/Sr39</i>	T2B/2S#2	Homoeol. rec.	C	RL5711
6	<i>Ae. longissima</i>	<i>Pm13</i>	T3BL.3BS-3S1#1S	Homoeol. rec.	C	RIA
7	<i>Ae. comosa</i>	<i>Yr8/Sr34</i>	T2DS-2 M#1L.2 M#1S	Homoeol. rec.	C	2D-2M#3/8
8	<i>Ae. geniculata</i>	<i>Lr57/Yr40</i>	T5DL.5DS-5MgS	Homoeol. rec.	C	TA5602
9	<i>Ae. triuncialis</i>	<i>Lr58</i>	T2BS.2BL-2IL	Spontaneous	C	TA5605
10	<i>Ae. umbellulata</i>	<i>Lr76/Yr70</i>	T5DL.5DS-5US	Homoeol. rec.	C	T393-4
11	<i>T. timopheevii</i>	<i>Sr36/Pm6<sup>a</sup></i>	T2B/2G#1	Homoeol. rec.	C	C747
12	<i>T. araraticum</i>	<i>Sr40</i>	T2BL/2G#2S	Homoeol. rec.	C	RL6087
13	<i>S. cereale</i>	<i>Pm8/Sr31/Lr26/Yr9<sup>a</sup></i>	T11BL.1R#1S	Spontaneous	C	WGRC14
14	<i>S. cereale</i>	<i>Lr25/Pm7</i>	T4BS.4BL-2R#1L	Irradiation	N	Transec
15	<i>S. cereale</i>	<i>H21</i>	T2BS.2R	Tissue culture	C	KS85HF011
16	<i>A. elongatum</i>	<i>Lr19/Sr25<sup>a</sup></i>	T7DS.7DL-7Ae#1L	Irradiation	C	Agatha
17	<i>A. elongatum</i>	<i>Sr24/Lr24<sup>a</sup></i>	T3DS.3DL-3Ae#1L	Spontaneous	C	Agent
18	<i>A. elongatum</i>	<i>Sr24/Lr24</i>	T1BL.1BS-3Ae#1L	Irradiation	N	Teewon
19	<i>A. elongatum</i>	WSMR	T4DS.4DL-1Ae#1L	Irradiation	N	CH5322
20	<i>A. intermedium</i>	<i>Wsm1</i>	T4DL.4A#2S	Irradiation	C	WGRC27
21	<i>A. intermedium</i>	BYDR	T7DS-7A#1S.7A#1L	Tissue culture	C	TC/e

<sup>a</sup>Commercially exploited, \*C -Compensating, N -Non-compensating

located in the nucleus. GISH has been widely used to investigate the origin of genomes, chromosomes, and parental genomes in hybrids (Schwarzacher et al. 1989) and to analyze derived introgressed lines from interspecific crosses (Murata et al. 1992; Schwarzacher et al. 1992; Taketa et al. 1997). Technical advances in DNA probe labeling, in situ hybridization and microscopy, allow repeated hybridization, mapping, and processing of chromosome images for multiprobe mapping on a single metaphase.

C-banding and GISH patterns detected alien introgression carrying *Lr9*, the first alien-resistant gene transferred from *Ae. umbellulata* into wheat, on chromosome 6B (Friebe et al. 1996). Alien introgressions carrying leaf and stripe rust resistance genes *Lr57* and *Yr40* from *Ae. geniculata* have been characterized by GISH (Kuraparthi et al. 2007a). One of the introgression lines (IL) had an alien translocation covering complete short arm and half of the long arm of chromosome 5D. Another IL had a small translocation spanning 1/4th of the short arm of 5D while the third IL did not show any GISH signal indicating that the alien segment was very small. Schwarzacher et al. (1992) used fluorescent in situ hybridization (FISH) technique to identify alien chromatin from *H. vulgare*, *Th. bessarabicum*, *Leymus muticaulis*, and *S. cereale* in chromosome spreads of wheat. Radiation-induced wheat-rye translocation lines resistant to Hessian fly were analyzed by the total genomic and highly repetitive rye DNA probes (Mukai et al. 1993). FISH analysis revealed the exact locations of the break points and allowed the estimation of the sizes of the transferred rye segments. Wheat-rye 1B-1R translocation has also been characterized by GISH (Heslop-Harrison et al. 1990). Using biotin labeled total genomic DNA of rye as probe for in situ hybridization, the sizes and 1B-1R translocation points in five wheat varieties were determined. All translocation break points were found to be at or near to centromere.

## 12.7 Molecular Markers for Characterization of Alien Introgressions

Molecular markers are useful tools for assaying genetic variation and provide an efficient means to link phenotypic and genotypic variations (Varshney et al. 2005). Using molecular markers, high-density genetic linkage maps in various crops have been established which in turn provide a basis for marker-assisted selection (MAS) of agronomically useful traits, for the pyramiding of the genes of interest and their isolation by map-based cloning.

Restriction fragment length polymorphism (RFLP) was one of the first DNA marker techniques used to characterize wheat cultivars (Vaccino et al. 1993). The polymerase chain reaction (PCR) technique facilitated the development of simpler and low-cost molecular markers, called SSR (also called microsatellites, Tautz and

Renz 1984). PCR-based markers, RAPD (Random Amplified Polymorphic DNA), STS (Sequence Tagged Sites), and SSR (Simple Sequence Repeat), etc. have been found to be invaluable tools for the monitoring of introgressed genes from different wild relatives into cultivated species (Autrique et al. 1995; Brown et al. 1996). Autrique et al. (1995) used RFLP markers to mark the resistance genes *Lr9* from *Ae. umbellulata* and *Lr32* from *Ae. tauschii*. RAPD markers were used to identify addition lines of *Ae. searsii* (Diaz-Salazar and Orellana 1995) and *Ae. caudata* (Peil et al. 1998).

Molecular markers are powerful tools for identifying quantitative traits and dissecting these complex traits into Mendelian factors in the form of quantitative trait loci (QTL) as well as for establishing the genomic locations of such genetic loci. Bulk segregant analysis (BSA), which involves pooling of entries at the two extremes for a segregating trait (Michelmore et al. 1991), has been effectively used for identifying molecular markers associated with disease-resistant genes in a number of species.

Various molecular markers have been widely used to tag and map resistance genes in wheat; however, SSRs have emerged as the choice of marker in gene-mapping studies. This type of molecular marker is genome-specific, appears to be evenly distributed over the wheat genome, and shows a higher level of polymorphism compared to any other marker system (Röder et al. 1998).

Microsatellite markers have been developed and incorporated in already-existing RFLP linkage maps in crops such as wheat (Roder et al. 1998). Wheat has more than 3000 SSR markers mapped so far (Song et al. 2005). Molecular markers can be used for alien gene transfers and understanding the mechanism of gene transfer. The size of the smallest translocation with a particular trait can be revealed by molecular mapping using physically and/or genetically mapped markers. Several DNA markers closely linked with rust-resistant genes have also been developed. Such markers ensure selection of a target gene based on the presence of the linked genotype. The success of selection depends on the close genetic association and robustness of a given marker across different genetic backgrounds. The markers found to be closely linked with the rust-resistant genes transferred from wild species are listed in Tables 12.5 and 12.6.

Schachermayr et al. (1994) developed near isogenic lines (NILs) for the *Ae. umbellulata* leaf rust-resistant gene *Lr9* and used two linked RFLP markers (cMWG 684, PSR 546) to locate it on 6BL of wheat. Gold et al. (1999) converted an ISSR (inter-simple-sequence repeat) marker to a SCAR (sequence characterized amplified region) marker linked to the chromosome segment carrying *Lr35* and *Sr39*. Robert et al. (1999) identified one RAPD and one RFLP marker closely linked to the stripe rust-resistant gene *Yr17*. Gupta et al. (2006) reported tagging of leaf rust-resistant gene *Lr19* (7DL) of wheat derived from *Ag. elongatum* using RAPD and microsatellite markers. Sixteen RAPD markers were identified as linked to the alien gene *Lr19*. Feuillet et al. (1995) screened Thatcher NILs for *Lr1* (5DL)



**Table 12.5** List of leaf rust and stripe rust resistance genes, transferred from wild progenitor species and tagged with molecular markers

Gene	Source	Chromosome	Marker	References
<b>Leaf rust resistance genes</b>				
<i>Lr63</i>	<i>T. monococcum</i>	3AS	SSR	Kolmer et al. (2010)
<i>Lr21</i>	<i>Ae. tauschii</i>	1DS	RFLP/RGA-STS	Rowland and Kerber (1974) Huang and Gill (2001)
<i>Lr22a</i>	<i>Ae. tauschii</i>	2DS	SSR	Hiebert et al. (2007)
<i>Lr32</i>	<i>Ae. tauschii</i>	3D	SSR	Thomas et al. (2010)
<i>Lr39/Lr41</i>	<i>Ae. tauschii</i>	2DS	SSR	Raup et al. (2001) Singh et al. (2004)
<i>Lr40</i>	<i>Ae. tauschii</i>	1DS	SSR	Spielmeier et al. (2000)
<i>Lr42</i>	<i>Ae. tauschii</i>	1DS	SSR	Liu et al. (2013)
<i>Lr43</i>	<i>Ae. tauschii</i>	7DS	SSR	Hussien et al. (1997)
<i>Lr28</i>	<i>Ae. speltoides</i>	4AL	RAPD/TPSCAR/SSR	Cherukuri et al. (2005); Vikal et al. (2004)
<i>Lr35</i>	<i>Ae. speltoides</i>	2B	RAPD/TPSCAR	Seyfarth et al. (1999)
<i>Lr36</i>	<i>Ae. speltoides</i>	6BS	–	Gold et al. (1999)
<i>Lr47</i>	<i>Ae. speltoides</i>	7AS	CAPS/SSR	Helguera et al. (2003)
<i>Lr51</i>	<i>Ae. speltoides</i>	1BL	CAPS	Helguera et al. (2005)
<i>Lr66</i>	<i>Ae. speltoides</i>	3A	SCAR	Marais et al. (2009a, b)
<i>Lr53</i>	<i>T. dicoccoides</i>	6BS	SSR	Dadkhodaie et al. (2011)
<i>Lr61</i>	<i>T. turgidum</i>	6BS	AFLP	Herrera-Fossel et al. (2008)
<i>Lr64</i>	<i>T. dicoccoides</i>	6AL	SSR	Kolmer (2008)
<b>Stripe rust resistance genes</b>				
<i>Yr28</i>	<i>Ae. tauschii</i>	4DS	SSR	Singh et al. (2000a, b)
<i>Yr15</i>	<i>T. dicoccoides</i>	6BS		Sun et al. (1997)
<i>Yr35</i>	<i>T. dicoccoides</i>	6BS	SSR	Dadkhodaie et al. (2011)
<b>Stem rust resistance genes</b>				
<i>Sr2</i>	<i>T. turgidum</i>	3BS	SSR/STS	Mago et al. (2011)
<i>Sr13</i>	<i>T. turgidum</i>	1DL/IRS	SSR	Knott (1962), Simons et al. (2011)
<i>Sr21</i>	<i>T. monococcum</i>	2AL	Sequence-based markers	Chen et al. (2015)

(continued)

**Table 12.5** (continued)

Gene	Source	Chromosome	Marker	References
<i>Sr22</i>	<i>T. monococcum</i>	7AL	SSR	Oslon et al. (2010)
<i>Sr35</i>	<i>T. monococcum</i>	3AL	SSR	Saintenac et al. (2013)
<i>Sr33</i>	<i>Ae. tauschii</i>	1DL	SSR	Periyannan et al. (2013)
<i>Sr45</i>	<i>Ae. tauschii</i>	1DS	EST/SSR/AFLP	Periyannan et al. (2014)
<i>Sr46</i>	<i>Ae. tauschii</i>	2DS	–	Yu et al. (2011) Singh et al. (2011)
<i>Sr32</i>	<i>Ae. speltoides</i>	2AL, 2BL	SSR/EST	Mago et al. (2013a, b)
<i>Sr39</i>	<i>Ae. speltoides</i>	2B	SCAR	Gold et al. (2002) Mago et al. (2009)
<i>Sr47</i>	<i>Ae. speltoides</i>	2BL	SSR	Faris et al. (2008)
<b>Powdery mildew resistance genes</b>				
<i>Pm1b</i>	<i>T. monococcum</i>	7AL	STS	Hsam et al. (1998)
<i>Pm1c</i>	<i>T. monococcum</i>	7AL	RFLP/RAPD	Sears and Briggie (1969) Hartl et al. (1995)
<i>Pm4d</i>	<i>T. monococcum</i>	2AL	SSR/STS	Schmolke et al. (2012)
<i>Pm25</i>	<i>T. monococcum</i>	1A	RAPD	Shi et al. (1998)
<i>Pm2</i>	<i>Ae. tauschii</i>	5DS	SSR	Qiu et al. (2006)
<i>Pm19</i>	<i>Ae. tauschii</i>	7D	–	Lutz et al. (1995a, b)
<i>Pm34</i>	<i>Ae. tauschii</i>	5DL	SSR	Miranda et al. (2006)
<i>Pm35</i>	<i>Ae. tauschii</i>	5DL	SSR	Miranda et al. (2007)
<i>Pm1d</i>	<i>T. spelta</i> var. <i>duhamelianum</i>	7AL	STS	Hsam et al. (1998)
<i>Pm12</i>	<i>Ae. speltoides</i>	6BS	RFLP	Jia et al. (1996)
<i>Pm32</i>	<i>Ae. speltoides</i>	1BL	Monosomic	Hsam et al. (2003)
<i>Pm3 k</i>	<i>T. dicoccoides</i>	1AS		Yahiaoui et al. (2009)
<i>Pm16</i>	<i>T. dicoccoides</i>	4A	SSR	Chen et al. (2005)
<i>Pm26</i>	<i>T. turgidum</i> var. <i>dicoccoides</i>	2BS	RFLP	Rong et al. (2000)
<i>Pm30</i>	<i>T. dicoccoides</i>	5BS	–	Liu et al. (2002)
<i>Pm31</i>	<i>T. dicoccoides</i>	6AL	–	Xie et al. (2003)
<i>Pm36</i>	<i>T. dicoccoides</i>	5BL	EST	Blanco et al. (2008)
<i>Pm41</i>	<i>T. dicoccoides</i>	3BL	SSR/RFLP	Li et al. (2009)
<i>Pm42</i>	<i>T. dicoccoides</i>	2BS	SSR/RFLP	Hua et al. (2009a)

(continued)

**Table 12.5** (continued)

Gene	Source	Chromosome	Marker	References
<i>Pm5a</i>	<i>T. dicoccum</i>	7BL	SSR	Law and Wolfe (1966)
<i>Pm49</i>	<i>T. dicoccum</i>	2BS		Piarulli et al. (2012)
<i>Pm50</i>	<i>T. dicoccum</i>	2AL		Mohler et al. (2013)

**Table 12.6** List of leaf rust and stripe rust resistance genes, transferred from wild non-progenitor species and tagged with molecular markers

Gene	Source	Chromosome	Marker	References
Leaf rust resistance genes				
<i>Lr9</i>	<i>Ae. umbellulata</i>	6BL	STS/RFLP/RAPD/SCAR	Schachermayr et al. (1994)
<i>Lr76</i>	<i>Ae. umbellulata</i>	5DS	STS	Bansal et al. (2015)
<i>Lr18</i>	<i>T. timopheevi</i>	5BL	N-band	Yamamori (1994)
<i>Lr50</i>	<i>T. timopheevi</i> <i>subsp. armeniacum</i>	2BL	SSR	Brown-Guedira et al. (2003)
<i>Lr52</i>	<i>T. timopheevi</i> <i>subsp. viticulosum</i>	2A	SSR	Tar et al. (2008)
<i>Lr54</i>	<i>Ae. kotschyi</i>	2DL	SCAR	Marais et al. (2005)
<i>Lr59</i>	<i>Ae. peregrina</i>	1AL	SSR	Marais et al. (2008, 2010)
<i>Lr57</i>	<i>Ae. geniculata</i>	5DS	CAPS	Kuraparthi et al. (2009)
<i>Lr58</i>	<i>Ae. triuncialis</i>	2BL	SSR	Kuraparthi et al. (2011)
<i>Lr62</i>	<i>Ae. neglecta</i>	6AS	SSR	Marais et al. (2009a, b)
<i>Lr56</i>	<i>Ae. sharonensis</i>	6A	SSR	Marais et al. (2010a, b)
<i>Lr25</i>	<i>Secale cereale</i>	4BL	RAPD/SSR	Procurier et al. (1995, ) Singh et al. (2011)
<i>Lr26</i>	<i>Secale cereale</i>	1BL	RFLP	Mago et al. (2005a, b)
<i>Lr44</i>	<i>T. spelta</i>	1B	SSR	Dyck and Sykes (1994)
<i>Lr37</i>	<i>Ae. ventricosa</i>	2AS	SCAR/CAPS	Helguera et al. (2003)
<i>Lr38</i>	<i>Ag. intermedium</i>	2AL	SSR	Mebrate et al. (2008)

(continued)

**Table 12.6** (continued)

Gene	Source	Chromosome	Marker	References
<i>Lr19</i>	<i>Ag. elongatum</i>	7DL	RFLP/STS/RAPD	Prins et al. (2001) Gupta et al. (2006)
<i>Lr24</i>	<i>Ag. elongatum</i>	3DL	STS/SCAR	Dedryver et al. (1996) Gupta et al. (2006)
<i>Lr29</i>	<i>Ag. elongatum</i>	7DS	RAPD/SCAR	Procnier et al. (1995)
<i>Lr55</i>	<i>Elymus trachycaulis</i>	1B	Dart	Friebe et al. (2005)
<b>Stripe rust resistance genes</b>				
<i>Yr37</i>	<i>Ae. kotschy</i>	2DL	SCAR	Marais et al. (2005)
<i>Yr38</i>	<i>Ae. sharonensis</i>	6AL	SSR	Marais et al. (2010a, b)
<i>Yr40</i>	<i>Ae. geniculata</i>	5DS	CAPS	Kuraparthi et al. (2009)
<i>Yr42</i>	<i>Ae. neglecta</i>	6AS	SSR	Marais et al. (2009a, b)
<i>Yr8</i>	<i>Ae. comosa</i>	2A, 2D	–	Riley et al. (1968a, b)
<i>Yr5</i>	<i>T. spelta</i>	2BL	STS	McGrann et al. (2014)
<i>Yr17</i>	<i>Ae. ventricosa</i>	2AS	SCAR/CAPS	Robert et al. (1999)
<i>Yr70</i>	<i>Ae. umbellulata</i>	5DS	STS	Bansal et al. (2015)
<i>Yr9</i>	<i>S. cereal</i>	1BL/IRS	RFLP	Mago et al. (2005a, b)
<i>Yr50</i>	<i>Th. intermedium</i>	4BL	SSR	Liu et al. (2013)
<b>Stem rust resistance genes</b>				
<i>Sr34</i>	<i>Ae. comosa</i>	2A, 2D		Friebe et al. (1996)
<i>Sr36</i>	<i>T. timopheevi</i>	2BS	SSR	Tsilo et al. (2008)
<i>Sr37</i>	<i>T. timopheevi</i>	4BL	SSR	Zhang et al. (2012)
<i>Sr40</i>	<i>T. timopheevi</i>	2BS	SSR	Wu et al. (2009)
<i>Sr38</i>	<i>Ae. ventricosa</i>	2AS		Helguera et al. (2003)
<i>Sr53</i>	<i>Ae. geniculata</i>	5DL	RFLP	Liu et al. (2011)
<i>Sr27</i>	<i>Secale cereal</i>	3AS		Singh et al. (2011)
<i>Sr31</i>	<i>Secale cereal</i>	1BL		Mago et al. (2002)
<i>Sr50</i>	<i>Secale cereal</i>	1DL/IRS	–	Anugrawati et al. (2008)
<i>Sr24</i>	<i>Th. elongatum</i>	3DL	SSR	Mago et al. (2005a, b)
<i>Sr25</i>	<i>Th. elongatum</i>	7DL	STS	Liu et al. (2010)

(continued)

**Table 12.6** (continued)

Gene	Source	Chromosome	Marker	References
<i>Sr26</i>	<i>Th. elongatum</i>	6AL	STS	Mago et al. (2005a, b)
<i>Sr43</i>	<i>Th. elongatum</i>	7DL	SSR/EST	Xu et al. (2009)
<i>Sr44</i>	<i>Th. intermedium</i>	7DS		Liu et al. (2013)
<i>Sr52</i>	<i>Dasypyrum villosum</i>	6AL	SSR/RFLP	Qi et al. (2011)
<b>Powdery mildew resistance genes</b>				
<i>Pm1d</i>	<i>T. spelta</i> var <i>duhamelianum</i>	7AL	AFLP	Hsam et al. (1998)
<i>Pm4b</i>	<i>T. carthlicum</i>	2AL	SSR/STS	The et al. (1979)
<i>Pm33</i>	<i>T. carthlicum</i>	2BL	SSR/STS	Zhu et al. (2005)
<i>Pm3b</i>	<i>T. sphaerococcum</i>	1AS	SSR/RFLP	Yahiaoui et al. (2004)
<i>Pm7</i>	<i>S. cereale</i>	4BL	–	Friebe et al. (1994)
<i>Pm20</i>	<i>S. cereale</i>	6BS	–	Heun et al. (1990)
<i>Pm8</i>	<i>S. cereale</i>	1BL/1RS	STS	Mohler et al. (2001)
<i>Pm17</i>	<i>S. cereale</i>	1BL/1RS	RFLP	Mohler et al. (2001)
<i>Pm29</i>	<i>Ae. ovata</i>	7DL	RFLP/AFLP	Zeller et al. (2002)
<i>Pm13</i>	<i>Ae. longissima</i>	3B	STS/RFLP/RAPD	Ceoloni et al. (1992), Cenci et al. (1999)
<i>Pm6</i>	<i>T. timopheevii</i>	2B	RFLP	Jørgensen (1973)
<i>Pm27</i>	<i>T. timopheevii</i>	6B	SSR/RFLP	Jarve et al. (2000)
<i>Pm37</i>	<i>T. timopheevii</i>	7AL	SSR	Perugini et al. (2008)
<i>Pm40</i>	<i>Th. intermedium</i>	7BS	SSR	Luo et al. (2009)
<i>Pm43</i>	<i>Th. intermedium</i>	2DL	SSR	He et al. (2009)
<i>Pm21</i>	<i>Haynaldia villosum</i>	6AS	SCAR/RFLP	Qi et al. (1996)

with 37 RFLP probes and found three to be linked to the gene after testing on F<sub>2</sub> populations between Thatcher and *Lr1*/Thatcher. Helguera et al. (2003) developed PCR primers based on existing RFLP markers for the *Lr37–Yr17–Sr38* gene cluster.

*Lr57* and *Yr40*, a leaf rust and stripe rust resistance gene, respectively, introgressed from *Ae. geniculata* have been mapped on chromosome 5DS of wheat using 11 RFLP probes (Kuraparthy et al. 2007a). PCR-based CAPS markers were later developed by Kuraparthy et al. (2009) which are being used for marker-assisted transfer of these genes to other backgrounds. The leaf rust-resistant gene *Lr21* has been located onto chromosome 1D and successfully cloned by Huang et al. (2003) using RFLP and STS markers. The rust-resistant genes *Lr20–Sr15* (7AL) and *Lr47* (7AS) were mapped using STS, SSR, CAPS, and SCAR

**Table 12.7** Stripe rust QTLs on different chromosomes

QTL	Markers	References
<i>QPst.jic-1BL</i>	<i>Xgwm259-Xgwm818</i>	Melichar et al. (2008)
<i>QYr.uga-2AS</i>	<i>Xbarc124-Xgwm359</i>	Hao et al. (2011)
<i>QYr.sgi.2B.1</i>	<i>Xgwm148</i>	Ramburan et al. (2004)
<i>QYrl.cau-2BS.2</i>	<i>Xgwm148-Xbarc167</i>	Guo et al. (2008)
<i>QYrcaas-5AL</i>	<i>Xwmc410-Xbarc261</i>	Lan et al. (2010)
<i>QYrtm.pau-2A</i>	<i>Xwmc407-Xwmc170</i>	Chhuneja et al. (2008a)
<i>QYrtb.pau-5A</i>	<i>Xbarc151-Xcfd12</i>	Chhuneja et al. (2008a)
<i>QYr.tem-5B.2</i>	<i>Xwmc235-Xgwm604</i>	Feng et al. (2011)
<i>QYrst.wgp-6BS.2</i>	<i>Xgwm132-Xgdm113</i>	Santra et al. (2008)

markers (Purnhauser et al. 2000; Neu et al. 2002; Stepien et al. 2003, Khan et al. 2005). A leaf rust-resistant gene *Lr58* has been transferred from *Ae. triuncialis* L. into common wheat (*Triticum aestivum* L.). Using RFLP markers *XksuF11*, *XksuH16*, and *Xbg123*, the gene was mapped on distal region of chromosome arm 2BL (Kuraparthi et al. 2007b).

Stripe rust-resistant genes in diploid A genome were mapped and transferred to bread wheat. A linkage map with 169 SSR and RFLP loci generated from a set of 93 RILs from a cross involving *T. monococcum* (acc. pau14087) and *T. boeoticum* (acc. pau5088) was used for mapping stripe rust-resistant genes. The QTL-controlling stripe rust resistance in *T. monococcum* was mapped on chromosome 2A (*QYrtm.pau-2A*), whereas the QTL from *T. boeoticum* was mapped on 5A (*QYrtm.pau-5A*). One stripe rust-resistant gene from *T. boeoticum* acc. pau5088 was confirmed to be introgressed in cultivated wheat which was indicated by co-introgression of *T. boeoticum* sequences linked to stripe rust-resistant QTL, *QYrtb.pau-5A* (Chhuneja et al. 2008a). Some of the reported stripe rust QTLs are listed in Table 12.7.

## 12.8 Progenitor Gene Pool of Wheat—A Source for Disease Resistance

### 12.8.1 Diploid 'A' Genome Species

*Triticum monococcum* L., generally known as einkorn wheat, is an ancient diploid A genome wheat that was domesticated about 10,000 years ago in the southwest Turkey in the Karaca Dag mountains (Heun et al. 1997). *T. monococcum* ssp. *monococcum* L. is domesticated and *T. monococcum* ssp. *aegilopoides* (Link) Thell. *T. boeoticum* Boiss. ( $2n = 2x = 14$ ) is a wild form of *T. monococcum* ssp. *monococcum*. Primary gene pool of wheat, *T. monococcum* s.l., comprising three closely related species *T. monococcum*, *T. boeoticum*, and *T. urartu*, harbors

useful variability for many economically important genes, including resistance to diseases, which can be used for hexaploid wheat improvement (Feldman and Sears 1981; Dhaliwal et al. 1993; Hussien et al. 1997; Yao et al. 2007) but they have not been exploited to the level of the D genome or other *Aegilops* species have been exploited. *T. urartu* has been the A genome donor of the most important polyploid wheat species including the durum or macaroni wheat *T. turgidum* (AABB), *T. timopheevii* (AAGG), and common wheat *T. aestivum* (AABBDD). In contrast, *T. monococcum* has only been used for the generation of *T. zhukovskyi* ( $A^m A^m AAGG$ ) (Dvorak et al. 1993; Dubcovsky et al. 1995). Thus, the  $A^m$  genome is under-represented in hexaploid wheat, and the exploitation of genetic diversity in *T. monococcum* and discovery of novel variant alleles may provide opportunities for further wheat genetic improvement. There is advantage of introgressing traits from *T. monococcum* than other wheat relatives as introgressed chromatin from *T. monococcum* readily recombines with *T. aestivum* chromatin thus facilitating the transfer of traits into wheat germplasm with ease. This provides an opportunity to reduce the size of the alien chromatin and to eliminate linkage to unwanted genes.

*T. monococcum* has high levels of resistance to the wheat leaf rust. Though some reports suggested the low level of genetic variation in *T. monococcum*, Bai et al. (1998) studied 49 *T. monococcum* accessions for leaf rust and all were found to possess the same gene for leaf rust resistance. Anker and Niks (2001) reported most of the *T. monococcum* accessions (84 %) to be resistant, whereas all *T. urartu* accessions were found susceptible to leaf rust. *T. monococcum* and *T. boeoticum* were found to be closely related but their host status for the wheat leaf rust fungus clearly differed. These three diploid wheat species thus differed in their reaction to wheat leaf rust. This is more likely based on a high allele frequency of one or more effective major genes in *T. monococcum* which are absent in *T. boeoticum* hence, *T. monococcum* has almost a non-host status to the wheat leaf rust (Anker et al. 2001).

Several disease resistance genes have been transferred from *T. monococcum*, *T. boeoticum*, and *T. urartu* to cultivated wheat. A summary of the resistance genes for leaf rust, stripe rust, stem rust and powdery mildew transferred from A genome species and cataloged is summarized in Table 12.5. Valkoun et al. (1986) reported leaf rust resistance in three accessions of *T. boeoticum* and its transfer into hexaploid wheat. A single gene giving partial resistance to leaf rust was introduced from *T. monococcum* to Thatcher isogenic line RL6137 mapped on chromosome 3A. This gene in RL6137 on chromosome 3AS was designated as *Lr63* (McIntosh et al. 2009). Also, Hussien et al. (1997) mapped leaf rust-resistant genes in winter wheat lines derived from *T. boeoticum* on chromosomes 6A, 1A, and 5A.

Rouse and Jin (2011) screened 1061 accessions of *T. monococcum* and 205 accessions of *T. urartu* against five *P. graminis* f. sp. *tritici* races and found 78.7 % of *T. monococcum* and 93.0 % of *T. urartu* to be resistant to race TTKSK, however, only 6.4 % *T. monococcum* accessions were resistant to all the five races. Infection-type patterns of accessions of both species indicated previously uncharacterized genes for resistance to race TTKSK exist in both *T. monococcum* and *T. urartu*. Stem rust resistance genes, namely *Sr21* (2A), *Sr22* (7A) and *Sr35* (3A),

have been successfully transferred and mapped in common wheat from *T. monococcum* (Table 12.5; Paull et al. 1994; McIntosh et al. 1984).

Apart from rust resistance, powdery mildew resistance has also been introduced from *T. monococcum*. *Pm1* and its two alleles *Pm1b* and *Pm1c* have been transferred from *T. monococcum* into cultivated wheat (Sears and Brigggle 1969; Hsam et al. 1998; McIntosh et al. 2008). *Pm25* a major gene for powdery mildew resistance has been transferred to common wheat germplasm NC96BGTA5 from wild einkorn accession PI427662 and mapped on chromosome 1A in close association with gene *Pm3A* (Shi et al. 1998). Plamenov et al. (2009) produced amphiploid between two durum cultivars and the *T. monococcum* ssp. *aegilopoides* which showed resistance to powdery mildew at seedling and adult plant stage and to four leaf rust races at seedling stage showing that amphiploids of A genome and durum are valuable resource of fungal resistance. *Pm4d* from *T. monococcum* is another gene located on *Pm4* locus, which was found in *Tm27d2* cultivar (Schmolke et al. 2012). Monneveux et al. (2001) reviewed *T. monococcum* as a useful resource of several resistance genes for root rot (Yamaleev et al. 1989), scab (Saur 1991), *Septoria tritici* avenae (Yu and Sun 1995), nodorum (Ma and Hughes 1993), Hessian fly (Bouhssini et al. 1997) and aphids (Pietro et al. 1998).

At Punjab Agricultural University, Ludhiana, India, about 200 accessions of *T. monococcum* and *T. boeoticum* were screened for leaf rust and stripe rust resistance for several years and we found that all the *T. monococcum* accessions, most of the *T. boeoticum* and a few *T. urartu* accessions, were completely resistant to leaf rust. However, a lot of variation was observed for stripe rust resistance. Most of the *T. monococcum* accessions have shown moderate to complete resistance; most of the *T. boeoticum* accessions showed complete resistance and the majority of the *T. urartu* accessions were highly susceptible. The stripe rust data recorded during 2012–2013, 2013–2014, and 2014–2015 crop seasons and leaf rust data for 2013–2014 are summarized in Table 12.8.

A recombinant inbred line (RIL) population developed by crossing *T. boeoticum* acc. pau5088 with *T. monococcum* acc. pau14087 showed segregation for resistance to several diseases including stripe rust, powdery mildew, Karnal bunt, and cereal cyst nematode (Dhaliwal et al. 2003; Singh et al. 2007a). This population was used for generating a linkage map of the diploid A genome of wheat (Singh et al. 2007a, b) consisting of 179 SSR, RFLP, and bin-mapped EST markers (Fig. 12.3). Using this inter-subspecific map, we have mapped genes/QTLs for a number of wheat diseases including stripe rust, cereal cyst nematode, and Karnal bunt. Two QTLs, one each in *T. monococcum* acc. pau14087, and *T. boeoticum* acc. pau5088, were detected for resistance in the RIL population. The QTL in *T. monococcum* mapped on 2A in a 3.6 cM interval between *Xwmc407* and *Xwmc170*, whereas the QTL from *T. boeoticum* mapped on 5A in 8.3 cM interval between *Xbarc151* and *Xcfd12* (Chhuneja et al. 2008a, b, c).

With the objective of transferring these genes into hexaploid wheat, *T. monococcum* acc. pau14087 and one resistant RIL were crossed to hexaploid wheat, using *T. durum* as a bridging species. The F<sub>1</sub> triploid plants were crossed to

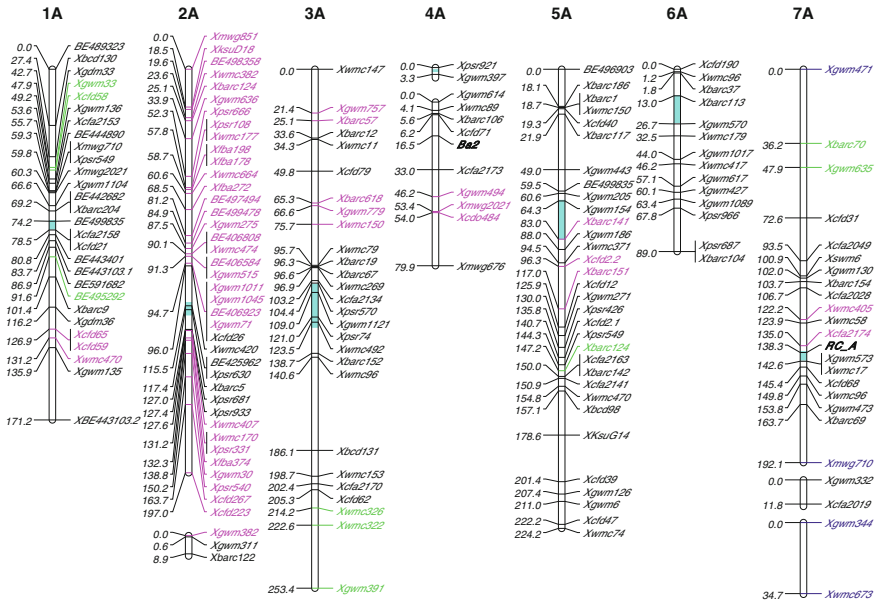


**Table 12.8** Rust reaction of different accessions of progenitor species of wheat recorded during 2012–2013 and 2013–2014 crop seasons under field conditions at Punjab Agricultural University, Ludhiana, India

Species	Year	Number of accessions			Total accessions
		Highly resistant <sup>a</sup>	Moderately resistant	Susceptible	
<b>Stripe rust</b>					
<i>T. monococcum</i>	2013	52	6	3	61
	2014	46	2	4	52
	2015	58	1	1	60
<i>T. boeoticum</i>	2013	58	6	9	73
	2014	157	3	14	174
	2015	153	4	14	171
<i>T. urartu</i>	2013	–	–	–	–
	2014	15	8	6	29
	2015	8	3	18	29
<i>Ae. tauschii</i>	2013	67	52	84	203
	2014	72	11	198	281
	2015	22	53	208	283
<i>Ae. speltoides</i>	2013	88	24	3	115
	2014	66	24	9	99
	2015	168	5	2	175
<i>T. diccoides</i>	2013	3	10	15	28
	2014	57	35	81	173
	2015	72	39	45	156
<b>Leaf rust</b>					
<i>T. monococcum</i>	2014	52	0	0	52
<i>T. boeoticum</i>	2014	166	0	8	174
<i>T. urartu</i>	2014	20	4	6	30
<i>Ae. tauschii</i>	2014	51	0	18	69
<i>Ae. speltoides</i>	2014	50	0	2	52
<i>T. diccoides</i>	2014	122	0	51	173

<sup>a</sup>The accessions with rust scores of 0, TR, and 5MR were categorized as highly resistant and those with 10MR–20MR and  $\geq 10S$  were categorized as moderately resistant and susceptible, respectively

susceptible hexaploid wheat cvs. WL711 and PBW343. In the F<sub>1</sub> triploid, only those gametes were viable to those have a full complement of A and B genomes (Gill et al. 1986). However, no resistant plants could be recovered in the backcross generations from this cross indicating that the resistance in diploid wheats was either recessive in nature or was being suppressed by the A and/or B genome of *T. durum*. The A genome of diploid wheat was expected to segregate in the F<sub>1</sub> of the cross *T. durum*/Tm14087/WL711 but not the B genome. The B genome of *T. durum*, however, was expected to segregate in the BC<sub>1</sub>F<sub>1</sub> generation of the cross *T.*

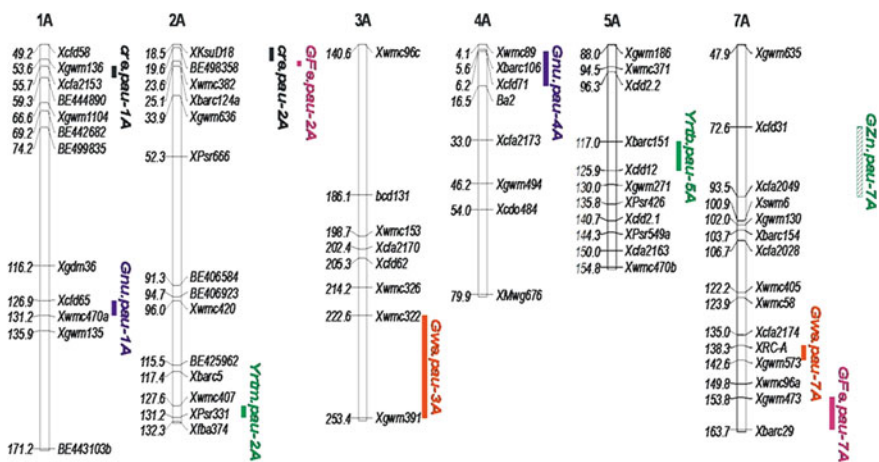


**Fig. 12.3** A-genome linkage map based on *T. boeoticum*/*T. monococcum* RIL population (Singh et al. 2007a, b)

*durum*/Tm14087//2\*WL711. If the B genome suppressed the resistance, then resistant plants were expected in this generation, which turned out to be true. Suppression of leaf and stripe rust-resistant genes in amphiploids generated by crossing susceptible *T. durum* and several accessions of *Ae. umbellulata* and *Ae. caudata* was also observed (Aghaee et al. 2001). The leaf rust- and stripe rust-resistant BC<sub>1</sub>F<sub>1</sub> plants were then allowed to self and stripe rust-resistant homozygous progenies with good plant type were developed.

*T. boeoticum*/*T. monococcum* RIL population showed digenic segregation for cereal cyst nematode resistance also. Composite interval mapping identified two QTLs, one each on chromosome 1AS and 2AS, conferring CCN resistance to *T. monococcum*. 1A QTL, designated as *Qcre.pau-1A*, appeared to be a major gene with 34 % contribution to the overall phenotypic variance (Singh et al. 2010). *Qcre.pau-1A* is a putative novel CCN resistance gene since this is the only CCN resistance gene mapped in any ‘A’ genome species and none of other known genes have been mapped on chromosome 1A. The other QTL mapped on 2A, designated as *Qcre.pau-2A*, might be allelic to *Cre5*, a CCN resistance gene transferred from *Ae. ventricosa* and mapped on 2AS almost in the same chromosomal region. *Qcre.pau-1A* was transferred to cultivated wheat using *T. durum* as bridging species. Selected CCN-resistant F<sub>8</sub> homozygous introgression lines with 2n = 28 and 2n = 42 also showed the co-introgression of the molecular markers identified to be linked with CCN resistance gene *Qcre.pau-1A* indicating that this gene itself can provide complete resistance to *H. avenae*.

*T. boeoticum* pau5088 showed resistance against a number of powdery mildew resistance isolates and *T. monococcum* pau14087 was completely susceptible. Inheritance studies in the RIL population *T. boeoticum* pau5088/*T. monococcum* pau14087 indicated the presence of two powdery mildew-resistant genes in *T. boeoticum* acc. pau5088. Analysis of powdery mildew infection and molecular marker data of the RIL population revealed that both powdery mildew-resistant genes are located on the long arm of chromosome 7A. Mapping was conducted using an integrated linkage map of 7A consisting of SSR, RFLP, STS, and DArT markers. These powdery mildew-resistant genes were tentatively designated as *PmTb7A.1* and *PmTb7A.2* (Chhuneja et al. 2012). The *PmTb7A.2* is closely linked to STS markers MAG2185 and MAG1759 derived from an RFLP probes which are linked to powdery mildew-resistant gene *Pm1*. This indicated that *PmTb7A.2* might be allelic to *Pm1*. The *PmTb7A.1*, flanked by a DArT marker *wPt4553* and an SSR marker *Xcfa2019* in a 4.3 cM interval, mapped proximal to *PmT7A.2*. *PmTb7A.1* is putatively a new powdery mildew-resistant gene. The powdery mildew-resistant genes from *T. boeoticum* have been transferred to cultivated wheat background through marker-assisted backcrossing, using *T. durum* as bridging species (Elkot et al. 2015). Besides disease-resistant genes, the RIL population also segregated for quality and domestication traits. The position of 13 QTL mapped so far in *T. boeoticum*/*T. monococcum* RIL population is summarized in Fig. 12.4. This population is the evidence of the level of variability captured in the A genome of the wild species of wheat as from only two accessions 13 new genes/QTL could be identified and mapped.



**Fig. 12.4** Summary of the QTLs detected in *T. boeoticum*/*T. monococcum* RIL population for cereal cyst nematode resistance, yellow rust resistance, grain number/spikelet, grain weight, grain Fe and Zn concentration

### **12.8.2 *Aegilops tauschii* the D Genome Donor of Wheat: A Mine of Biotic Stress Tolerance Genes**

*Aegilops tauschii* Coss., a diploid self-pollinating goatgrass species has contributed the D genome to common wheat. Hybridization of *Ae. tauschii* (DD) with tetraploid wheat, *T. turgidum* L. (AABB) about 7000 years ago, led to the development of hexaploid wheat *Triticum spelta* (L) Thell (AABBDD) from which common wheat evolved. The D genome of *Ae. tauschii* has much greater genetic diversity compared to the D genome of *T. aestivum*. The hybridization events that led to the evolution of bread wheat are thought to have involved only a few accessions of *Ae. tauschii*. In fact, *Ae. tauschii* represents more than 90 % of the total genetic variability present in the D genome (Lubbers et al. 1991). The morphological variation and ecological amplitude of *Ae. tauschii* exceeds that of any other diploid *Triticum* or *Aegilops* species (Zohary et al. 1969). Much of the genetic diversity in *Ae. tauschii* gene pool thus remained unutilized and may not be represented in the *T. aestivum* gene pool. Furthermore, the D genome of bread wheat has not undergone any major chromosomal restructuring in relation to the *Ae. tauschii* genome, ensuring high homology and ease of gene transfer. *Ae. tauschii* represents a rich reservoir of disease resistance (Dhaliwal et al. 1993; Villareal et al. 1994a, b; Cox 1998; Aseefa and Fehrman 2004), productivity traits (Waines et al. 1987) and abiotic stress resistance (Trethowan and Mujeeb-Kazi 2008).

Based on spikelet morphology, *Ae. tauschii* has been divided into two subspecies, *tauschii* and *strangulata*. ssp. *tauschii* has a very wide geographic distribution extending westward to Turkey and eastward to Afghanistan and China, whereas ssp. *strangulata* has a narrow distribution occurring only in two disjointed regions, in southeastern Caspian Iran and Transcaucasia (Kihara et al. 1965; Yen et al. 1983; Jakaska 1995). Subspecies *strangulata* has been proposed as the D genome donor of wheat. *Strangulata* has been reported to have higher level of resistance than ssp. *tauschii* (Yildirim et al. 1995; Knaggs et al. 2000; Liu et al. 2010). Kihara and Tanaka (1958) and Kihara et al. (1965) assessed seedling responses to all three rusts among 167 accessions of *Ae. tauschii* from Pakistan, Afghanistan, and Iran. Resistant accessions were found mainly in the forms *meyeri* and *strangulata* collected from the Caspian Sea area of Iran while all accessions from Afghanistan and Pakistan were susceptible.

A commonly used route to transfer genes from *Ae. tauschii* is a two-step process of producing synthetic wheat via tetraploid  $\times$  *Ae. tauschii* hybridization and colchicine doubling. These synthetics are then crossed to elite wheat lines and homologous recombination between *Ae. tauschii* and *T. aestivum* 'D' genome chromosomes can readily break undesirable linkages between target genes and alleles associated with linkage drag which might not be possible with introgressions from other species. CIMMYT recognized the potential of *Ae. tauschii* germplasm in broadening the gene pool of wheat and developed 1000 synthetics from 460 *Ae.*

*tauschii* accessions (Muzeeb-Kazi et al. 1987). These synthetics were later backcrossed to many CIMMYT and global elite breeding lines to introduce new variation for various morphological and agronomic traits (Villareal et al. 1994a, b), resistance to biotic stresses (Cox 1998; Ma et al. 1995) and abiotic stresses (Villareal et al. 2001). The synthetics were also shown to be diverse at the molecular level, and genetically distinct from cultivated wheats (Zhang et al. 2005).

Yellow rust-resistant gene *Yr28* is the only cataloged stripe rust resistance which has been derived from *Ae. tauschii*. It has been mapped on chromosome arm 4DS after its transfer to synthetic hexaploid wheat from *Ae. tauschii* (McIntosh et al. 2008, 2010; Singh et al. 2000a, b). Another gene temporarily designated as *YrAS2388* has been mapped on chromosome 4DS using an F<sub>2</sub> population between a resistant (*strangulata*) and susceptible *Ae. tauschii* accessions but this gene showed partial resistance when transferred in synthetic hexaploid wheat background (Huang et al. 2011).

*Lr21* was transferred from *Ae. tauschii* accession TA1599 via a synthetic wheat (Rowland and Kerber 1974). This gene has been cloned from *Ae. tauschii* only (Huang et al. 2003). *Lr21* provides resistance to the current spectrum of *P. triticina* races in the Southern Great Plains. There are no confirmed reports of virulence to *Lr21*. *Lr1* is widespread in *Ae. tauschii* though there is no record of its transfer from *Ae. tauschii*; it may probably transferred to wheat at the time of the origin of wheat (Ling et al. 2004). Similarly, the *Lr34* haplotype was not detected in *Ae. tauschii*, and this gene probably arose during the few thousand years since the origin of common wheat (Gill et al. 2008).

An alternative method to transfer genes from *Ae. tauschii* is the direct hybridization between *Ae. tauschii* and *T. aestivum*. Combining gene transfer, genomic localization, and introgression (Olson et al. 2013) is an efficient method of expediting transfer of genes from *Ae. tauschii* into wheat-breeding germplasm. Adverse genetic interactions between the D genome of *Ae. tauschii* and the ABD genome of hexaploid wheat are uncommon (Gill and Raupp 1987). *Pm19* and *Pm34* (Lutz et al. 1995a, b; Miranda et al. 2006) were transferred from *Ae. tauschii* into cultivated wheat. *Pm2* was physically mapped to chromosome 5DS by McIntosh and Baker (1970). *Pm35* is another gene derived from *Ae. tauschii* direct crosses with hexaploid wheat and is mapped on chromosome 5DL (Miranda et al. 2007).

Many leaf rust resistance genes have been identified in the *Ae. tauschii* including *Lr22a* (2DS), *Lr32* (3D), *Lr39/Lr41* (2DS), *Lr42* (1D) (Cox et al. 1994; Gill et al. 1991; Kerber 1987; Hiebert et al. 2007; Huang and Gill 2001; Huang et al. 2003; Rowland and Kerber 1974; Raupp et al. 2001) which were transferred to hexaploid wheat germplasm and later on mapped onto specific chromosomes (Table 12.5). Recently, new flanking markers have been identified in vicinity of *Lr42* which will aid in MAS of this gene (Liu et al. 2013). *Lr21* and *Lr39* have been introgressed from *Ae. tauschii* ssp. *tauschii* and *Lr22a* and *Lr42* from ssp. *strangulata* (McIntosh et al. 2013). Two stem rust resistance genes such as *Sr33* and *Sr45* and powdery mildew resistance genes such as *Pm2* and *Pm19* have been transferred from *Ae. tauschii* (Hsam and Zeller 2002; Marais et al. 1998; McIntosh et al. 2013). Two

germplasm lines were developed carrying genes *Pm34*, *Pm35* also from *Ae. tauschii* (Miranda et al. 2006, 2007) and mapped on chromosome 5D (Table 12.5).

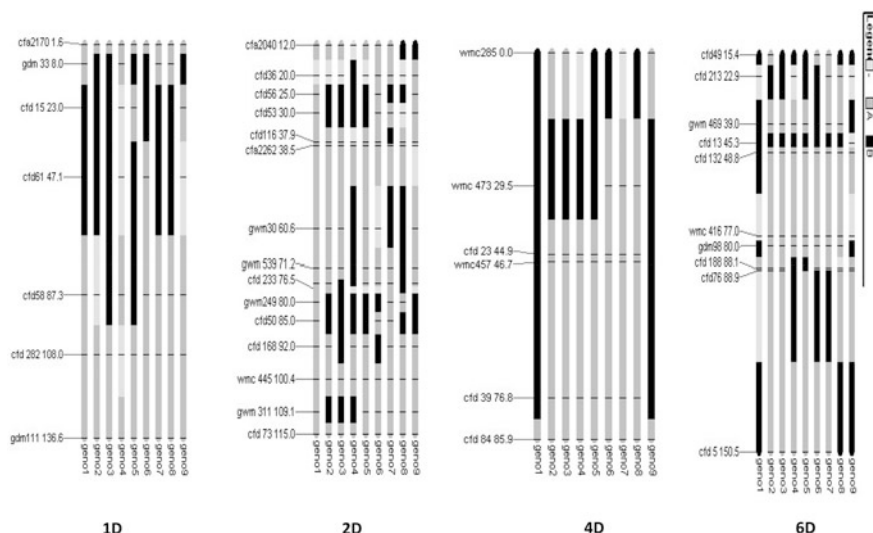
At Punjab Agricultural University, Ludhiana, India, we are maintaining an active collection of 280 *Ae. tauschii* accessions. These accessions have been found to carry resistance genes for various biotic stresses including leaf rust, stripe rust, powdery mildew, and Karnal bunt. Stripe rust reactions of these accessions over last five years have shown a lot of variation in the rust reaction. Reaction of the stripe rust resistant accessions of *Ae. tauschii* varied from totally immune to traces of resistance (TR), moderately resistant, and moderately susceptible.

The stripe rust and leaf rust data of these accessions are summarized in Table 12.8. In 2013, 67 out of 203 accessions showed high level of stripe rust resistance and 52 were moderately resistant while in 2014 out of 281 accessions, 72 were highly resistant and 11 moderately resistant. Genome-wide Association studies based on SNP markers identified eight significant loci ( $p < 0.01$ ) mapped on chromosome 7DL, 3DS, 2DS, 5DL for stripe rust resistance (our unpublished data). One of the accession pau14195 with multiple disease resistance was crossed with durum wheat cultivar PBW114 and resulting  $F_1$  was crossed and backcrossed with leaf rust, stripe rust, and KB susceptible cultivar WH542 for transferring leaf rust and stripe rust resistance genes to hexaploid wheat background. One gene for leaf rust resistance and linked non-glaucousness was mapped on chromosome 2D in hexaploid background (Saluja personal communication).

*Ae. tauschii* has a very high level of KB resistance also and a subset of *Ae. tauschii* germplasm was screened for KB resistance. Over three years of screening under artificial inoculations, 20 accessions were identified to be resistant to KB and six accessions were moderately resistant (Chhuneja et al. 2008c). Almost 80 % of the KB-resistant accessions belonged to *ssp. tauschii* which is contrary to the rust resistance where almost 90 % of the resistant accessions belonged to *ssp. strangulata* (Chhuneja et al. 2010). For the transfer of KB resistance to cultivated wheat, an amphiploid was synthesized by crossing a KB-resistant *Ae. tauschii* acc. pau 3743 with KB susceptible *T. durum* cultivar WH890. The synthetic hexaploid was crossed with a KB susceptible hexaploid wheat cv. to transfer KB resistance to desirable agronomic background and homozygous introgression lines were developed (ILs). Introgressions of *Ae. tauschii* specific alleles were found on chromosomes 1D, 2D, 4D, and 6D (Fig. 12.5) which indicated that the KB resistance gene (s) may be located on these regions.

### 12.8.3 *Ae. Speltoides and Other S Genome Species*

*Ae. speltoides* has depicted very high levels of disease resistance for leaf rust and stripe rust from screening over many years in PAU, Ludhiana. Leaf and stripe rust data for 2012–2013 and 2013–2014 crop seasons recorded under field conditions is



**Fig. 12.5** Graphical genotyping of wheat–*Ae. tauschii* introgression lines using D genome-specific SSR markers. *Gray areas* represent wheat-specific alleles and *black areas* indicate introgression of *Ae. tauschii*-specific alleles on chromosomes 1D, 2D, 4D, and 6D. Map distances are according to Komugi composite wheat map

presented in Table 12.8. Leaf rust resistance genes *Lr28*, *Lr35*, *Lr36*, *Lr47*, *Lr51*, *Lr54*, and stem rust resistance genes *Sr32*, *Sr39*, *Sr47* have been transferred from different accessions of *Ae. speltoides* by different workers (Table 12.5; McIntosh et al. 2013). Leaf rust resistance gene *Lr28* located on chromosome 4AL was transferred from *Aegilops speltoides* into wheat by Riley et al. (1968b). It was subsequently backcrossed into different wheat backgrounds in India (Tomar and Menon 1998) and it provides effective resistance against all the Indian leaf rust pathotypes. The stem rust resistance gene *Sr39* was transferred to the hexaploid wheat cultivar Thatcher (Tc) from *Ae. speltoides*. The gene is also associated with adult plant leaf rust resistance gene *Lr35* which is highly effective against North American populations of *P. recondita* f. sp. *tritici*. Both the *Sr39* and the *Lr35* genes are located on the alien translocated segment on chromosome 2BS (Niu et al. 2011). *Sr47*, also from *Ae. speltoides*, has been mapped in durum wheat–*Ae. speltoides* chromosome translocation line T2BL-2SL&2SS which is different from *Sr32* and *Sr39* located in the same region of 2BS (Faris et al. 2008). Gene *Pm12* originating from *Ae. speltoides* is located on T6BS-6SS-6SL (Miller et al. 1988; Jia et al. 1996).



### 12.8.4 *Non-progenitor Aegilops Species for Transfer of Disease-Resistant Genes to Hexaploid Wheat*

The genus *Aegilops* consists of 22 species of which 10 are diploid, 10 are tetraploid, and 2 are hexaploid with basic chromosome number  $x = n = 7$  and six different genomes as C, D, M, N, S, and U (van Slageren, 1994). *Aegilops* represents the largest part of the secondary gene pool of wheat and several species have been used in crop improvement programs. Non-progenitor *Aegilops* species with one of the genome as U has been found to be rich source of resistance genes (Mamluk and van Slageren 1994). *Ae. umbellulata* (UU), *Ae. geniculata* (UM), *Ae. triuncilais* (UC), *Ae. peregrina* (US), *Ae. kotschy* (US), etc. are valuable sources of useful genes for wheat breeding. *Ae. caudata* (C), *Ae. comosa* (M), *Ae. uniaristrata* (NN) are also known to be rich sources of resistance to various pathogens and pests (Pasquini 1980; Gill et al. 1985; Manisterski et al. 1988; Anikster et al. 2005). Many genes conferring resistance to rust diseases, powdery mildew, cereal cyst nematode, and insect pests were transferred from *Aegilops* species into wheat (Jiang et al. 1994; Friebe et al. 1996; Dhaliwal et al. 2003; Marais et al. 2005; Kuraparthy et al. 2007a, b; Chhuneja et al. 2008a, b; Riar et al. 2012).

Some leaf rust and stripe rust resistance genes transferred from wild non-progenitor species to cultivated wheat have been shown in Table 12.6. Some of the genes for disease resistance transferred from distantly related species have been exploited commercially but others seem to be associated with reduced yield due to linkage drag (Young and Tanksley 1989). The most successful example of alien genome segment transfer is wheat-rye translocation. In this wheat chromosome, 1BL was replaced by rye chromosome 1RS. The 1RS arm in this translocation has many genes such as *Lr26* for leaf rust resistance, *Sr31* for stem rust resistance, *Yr9* for stripe rust resistance (Bartos and Bares 1971; Bartos et al. 1973, b), and *Pm8* for powdery mildew resistance. This translocation has been incorporated into 60 wheat varieties, including the prominent Veery lines, that occupied 50 % of all developing country wheat area, almost 40 million hectares. Translocation T3DS.3DL-3Ae#1L from *Agropyron elongatum* carrying *Lr24/Sr24* is the second most exploited alien introgression. *Lr9* from *Ae. umbellulata*, *Sr26*, *Lr19* and *Sr25* from *Ag. elongatum* have also been exploited to some extent.

In the past several years, about 20 stem rust, 30 leaf rust, 10 stripe rust, and 15 powdery mildew resistance genes have been transferred from near and distant relatives of hexaploid wheat. Stem rust-resistant genes transferred from the tertiary gene pools of wheat include *Sr24* from *Agropyron elongatum*; *Sr31*, *Sr1*, and *Sr50* (Anugrahwati et al. 2008) from *Secale cereale*; *Sr36* from *T. timopheevii* (Olson et al. 2010); *Sr38* from *Ae. ventricosa* (McIntosh et al. 1995a, b); *Sr26* from *A. elongatum*; and *Sr44* from *A. intermedium* (Liu et al. 2013). Stem rust resistance genes *Sr51*, *Sr52*, and *Sr53* transferred from the tertiary gene pool were identified in chromosome addition lines and Robertsonian translocations from *Ae. searsii*, *Dasypryum villosum*, and *Ae. geniculata*, respectively (Liu et al. 2011; Qi et al. 2011).



Mwale et al. (2014) reviewed all the cataloged and uncataloged genes of powdery mildew resistance from wild progenitor of wheat. Hsam et al. (1998) reported the presence of allele *Pm1d* in *T. spelta*. *Pm4a* and *Pm4b* on chromosome 2AL were first reported by The et al. (1979) on cultivars Khapli (*T. dicoccum*) and Armada (*T. carthlicum*), respectively, and subsequently reviewed by Huang and Roder (2004) and Alam et al. (2011). Alleles of *Pm5* were identified and mapped on wheat chromosome 7BL. These include gene *Pm5a* in the wheat cultivars Hope, and a recessive gene that originated from *T. dicoccum* L. *Pm5c* was derived from *T. sphaerococcum* var. *rotundatum* (Hasm et al., 2001). *T. diccoides* is another important donor of powdery mildew resistance genes as *Pm26*, located on chromosome 2BS (Rong et al. 2000), *Pm42* (Hua et al. 2009a), and *Pm49*, located on chromosome 2BS were originated from *T. diccoides*. Other resistance genes transferred from *T. diccoides* include *Pm16*, *Pm30*, *Pm31*, *Pm36*, *Pm41*, *Pm42*, *Pm49*, and *Pm50*, located on chromosomes 4A, 5B, 6A, 5B, 3B, 2B, and 2A, respectively (Piarulli et al. 2012; Mohler et al. 2013a). *Pm6* is originated from the 2G chromosome of *T. timopheevii* and was introgressed into chromosome 2BL of common wheat (Tao et al. 2000). *T. carthlicum* is another wild relative source of powdery mildew-resistant genes. They include genes *Pm4b* and *Pm33* (Zhu et al. 2005). *Secale cereale*, a distant relative of common wheat also contributed *Pm7*, *Pm8*, *Pm17*, and *Pm20* genes to common wheat (McIntosh et al. 2011). Two designated genes *Pm40* and *Pm43* were introgressed into common wheat from *Elytrigia intermedium* and *Th. intermedium*, respectively (Luo et al. 2009; He et al. 2009) while *Pm21* originated from *Haynaldia villosum* (Chen et al. 1995; Piarulli et al. 2012; Xiao et al. 2013).

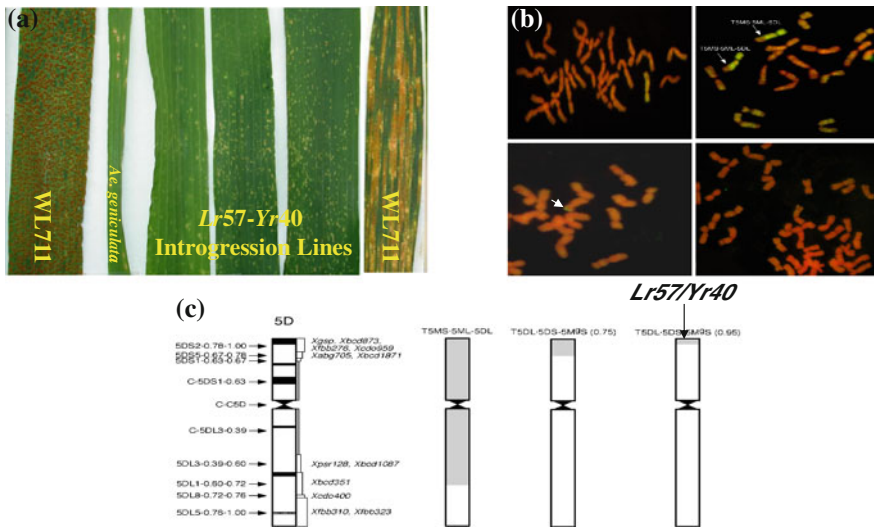
Ernie Sears (1956) used *Ae. umbellulata* for the transfer of leaf rust resistance to wheat. He presented this remarkable work at the 1956 Brookhaven Symposium. This commenced with the addition to *T. aestivum* of a single chromosome of *Ae. umbellulata* which also carried a number of undesirable genetic information. Sears X-rayed addition line carrying *Ae. umbellulata* chromosome with leaf rust resistance. The irradiated plants were then used to pollinate normal wheat and resistance progeny was selected. Forty of these had one of at least seventeen different translocations between the *Aegilops* chromosome and the wheat chromosomes. There was one line with the resistance chromosome segment apparently incorporated in the form of an intercalary translocation. Further work, published in 1966, showed that the *Ae. umbellulata* segment was not in an intercalary position but that a long *Aegilops* segment had replaced the terminal part of the long arm of wheat 6B. This gene was later on designated as *Lr9*. The gene *Lr9* derived from *Ae. umbellulata* is a highly effective gene throughout the world except in North America (Shaner et al. 1972) and in Canada (Samborski and Dyck 1976). Another important leaf rust-resistant gene *Lr24* is tightly linked to stem rust-resistant gene *Sr24* on the long arm of the chromosome 3D. Both resistance genes were introduced from *Ag. elongatum* in a spontaneous translocation involving 3Ag from *Agropyron* and 3DL from wheat. The alien segment carrying *Lr24/Sr24* does not impose any deleterious effect on yield as several cultivars carrying *Lr24* have been released for cultivation in India.

Evaluation of the wild *Aegilops* species belonging to secondary and tertiary gene pool over many years led to the identification of potential sources of

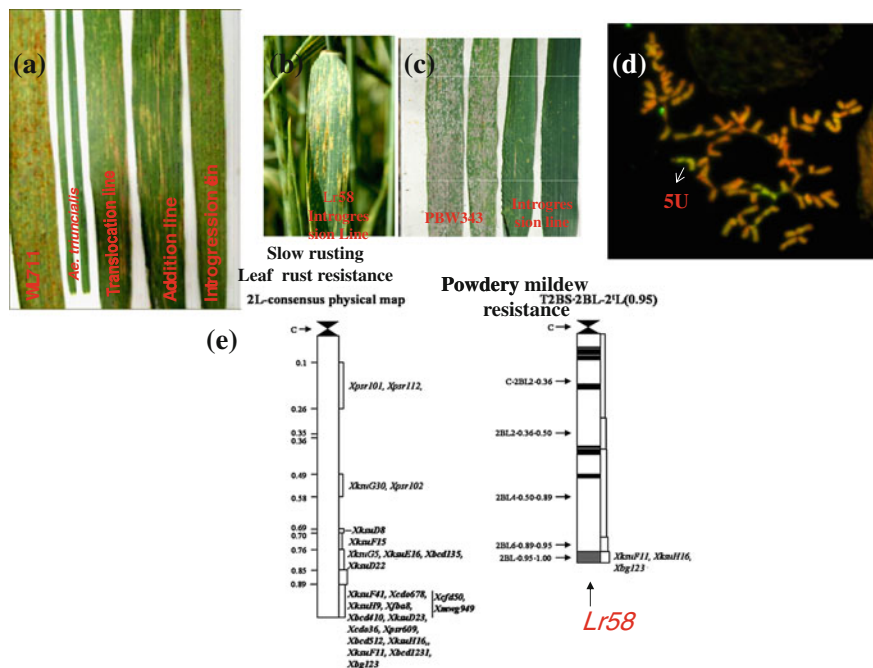
disease-resistant genes. The number of resistant accessions varied from year to year. One of the reasons could be change in the pathotype specificity which was observed in some other wheat lines also known genes.

### 12.9 Transfer of Rust Resistance Genes from Non-progenitor *Aegilops* Species

A leaf rust- and stripe rust-resistant disomic substitution line {DS5 M(5D)} with 5 M chromosome of *Ae. geniculata* substituted for 5D of wheat was developed through restricted backcrossing and selfing. The rust resistance of *Ae. geniculata* was transferred to wheat by induced homoeologous chromosome pairing between chromosomes 5 Mg of *Ae. geniculata* and 5D of wheat. The introgression lines were developed by crossing disomic substitution line DS 5 Mg(5D) with the Chinese Spring (CS) *Ph<sup>1</sup>* stock (Chen et al. 1994) and crossing the F<sub>1</sub> with susceptible bread wheat cultivar WL711. Advanced backcross lines were characterized using molecular cytogenetic and molecular techniques, and translocation carrying these leaf and stripe rust-resistant genes was mapped on distal end of 5DS (Fig. 12.6). These co-segregating genes have been designated as *Lr57* and *Yr40* (Kuraparthi et al. 2007a; McIntosh et al. 2008). This translocation encompassing ~3.5 % of 5DS is the smallest alien introgression characterized so far.



**Fig. 12.6** Transfer and mapping of leaf rust and stripe rust resistance genes *Lr57-Yr40* introgressed from *Aegilops geniculata* (UUMM) through induced homoeologous pairing in *T. aestivum*. **a** Leaf and stripe rust reaction **b** Genomic in situ hybridization **c** mapping of *Lr57*, *Yr40* in introgression lines (Kuraparthi et al. 2007a, b)

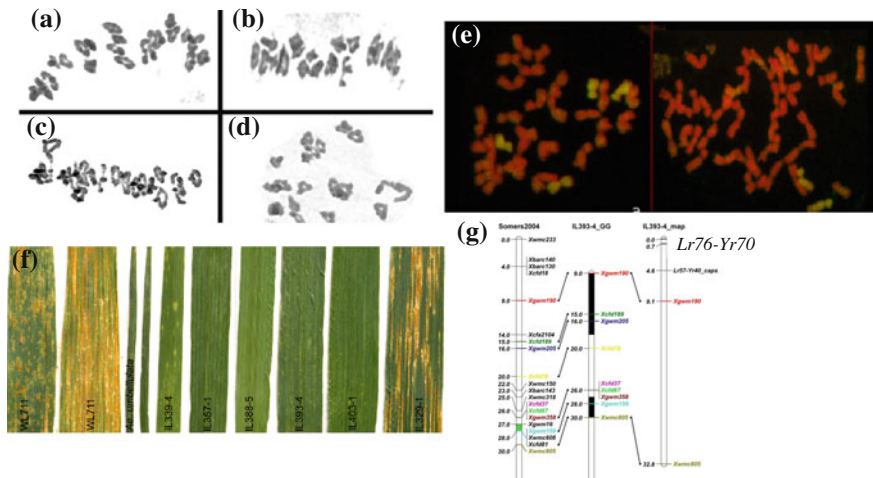


**Fig. 12.7** a Leaf rust reaction of wheat–*Ae. triuncialis* translocation, addition, and introgression lines; b Slow rusting for leaf rust in wheat–*Ae. triuncialis* substitution line 5U-5A; c powdery mildew resistance in PBW343–*Ae. triuncialis* introgression lines; d Genomic in situ hybridization of wheat–*Ae. triuncialis* 5U-5A substitution line; e mapping of *Lr58* introgressed from *Ae. triuncialis* through spontaneous translocation and characterized using molecular markers in wheat–*Ae. triuncialis* translocation line (Kuraparthi et al. 2007b)

PCR-based markers for these genes have also been developed. The introgression line with the smallest introgression carrying *Lr57-Yr40* is being used as a donor parent for mobilizing these genes to elite wheat backgrounds using MAS.

Similarly, a spontaneous translocation line developed from a cross of WL711 and *Ae. triuncialis* acc. 3549 was resistant to the most prevalent races of leaf rust in India. Genetic mapping in a segregating F<sub>2:3</sub> population showed that the rust resistance was monogenically inherited. Molecular analysis identified homeologous group 2 carrying the gene in question. The *Ae. triuncialis*-specific alleles of *XksuH16*, *XksuF11*, *Xbg123*, and one simple sequence repeat marker *Xcfd50* co-segregated with the rust resistance, suggesting that the wheat–*Ae. triuncialis* translocation occurred in the distal region of chromosome arm 2BL (Fig. 12.7 a,e) and was designated *Lr58* (Kuraparthi et al. 2007b).

From the same accession of *Ae. triuncialis* pau3549, a substitution line with resistance to leaf rust (slow rusting), powdery mildew, and cereal cyst nematode has also been developed. Alien chromosome in the WL711–*Ae. triuncialis* substitution line has been identified as 5U through C-banding . GISH studies also identified a satellite chromosome in the substitution line (Fig. 12.7 b,c,d). An alien addition line



**Fig. 12.8** **a–c** Meiotic analysis in wheat–*Ae. umbellulata* introgression lines; **d** Meiotic analysis in  $F_1$  plant from the cross of IL393-4 with bread wheat cv. PBW343; **e** Genomic *in situ* hybridization of WL711–*Ae. umbellulata* addition lines; **f** Leaf rust and stripe rust reaction of WL711, *Ae. umbellulata*, and six different WL711–*Ae. umbellulata* introgression lines; **g** Molecular mapping of *Lr76-Yr70* transferred from *Ae. umbellulata* through induced homoeologous pairing in IL 393-4

from the same cross has resistance for leaf rust, powdery mildew, and Karnal bunt. Karnal bunt and powdery mildew resistance has been transferred from the alien chromosome to the wheat cultivar PBW343.

Leaf and stripe rust resistance genes have also been introgressed from diploid species *Ae. umbellulata* and *Ae. caudata* using *T. durum* as bridging species (Chhuneja et al. 2008b; Riar et al. 2012). Rust resistance of *Ae. umbellulata* was transferred to wheat by homoeologous pairing between *Ae. umbellulata* and wheat chromosomes. The resistant plants were backcrossed 2–3 times with a susceptible wheat cv. WL711 followed by selfing to develop homozygous introgression lines with a high level of resistance to leaf rust as well as stripe rust. One of these introgression lines was crossed with *T. aestivum* cv. PBW343 to generate a mapping population, and a BC-RIL population was developed which segregated for a single gene each for leaf rust and stripe rust resistance. Both the rust resistance genes, however, co-segregated and were mapped on short arm of wheat chromosome 5D (Fig. 12.8) and have been designated as *Lr76* and *Yr70* (Bansal et al. 2015). Similar strategy was used for transfer of leaf and stripe rust resistance from *Ae. caudata*. Two genes one each for leaf rust and stripe rust were again mapped on chromosome 5DS. The stripe rust resistance gene transferred from *Ae. caudata* was found to be an adult plant resistance gene (Riar et al. 2012; Kaur 2014).

Two leaf rust and one stripe rust resistance genes have also been transferred from a tetraploid non-progenitor species *Ae. peregrina* to wheat cultivar WL711 through induction of homoeologous pairing. *Ae. peregrina* accession pau3519 was crossed with Chinese Spring stock carrying inhibitor of *Ph<sup>1</sup>* locus,  $F_1$  was crossed with

WL711 and advance backcross introgression lines developed. Molecular mapping in two different introgression lines identified one leaf rust resistance gene on 2DL and a pair of linked leaf and stripe rust resistance genes on 5DS.

## 12.10 R Gene Clusters from Alien Germplasm

Most of the resistance genes introduced from wild progenitor and non-progenitor of wheat are major/race-specific genes. The short-lived nature of race-specific leaf rust resistance genes greatly compromises the efforts of scientists and breeders. Alternatively, a more durable form of resistance is attributed to slow leaf-rusting or durable resistance in the form of retarded disease progress in the field results from a longer latent period, smaller pustule size, and lower spore production (Ohm and Shaner 1976 ; Wilcoxson 1981 ; Das et al. 1992 ). These genes confer a slow rusting type of resistance (Caldwell 1968 ) despite a compatible host reaction and are effective across all races of the pathogen, and disease reaction is measured several times during the course of disease in a growing season as Area Under Disease progress Curve (AUDPC) (Jeger and Viljanen-Rollinson 2001 ). So far only five resistance gene blocks, Lr34/Yr18/Pm38/Sr57, Lr46/Yr29/Pm39/Sr58, Sr2/Yr30 Lr67/Yr46/Pm46/Sr55, and Lr68 known for partial but durable resistance; however, none is from wild wheat (Singh et al. 2000a , b ; Hiebert et al. 2010 ; Herrera-Foessel et al. 2011; Singh et al. 2011 ). Main reason of wild germplasm contributing major genes is their tedious process of resistance gene transfer into cultivated wheat involving the use of bridging cultivars, many crosses and backcrosses, selecting resistant plants throughout the process, and maintain recurrent parent background. This ends up transferring only major genes, as in most of the cases resistance genes are mapped after their transfer into cultivated backgrounds.

Genes from wild germplasm are inherited as blocks of multiple disease resistance due to the absence of recombination from alien chromosomal segments such as gene cluster *Lr26/Yr9/Sr31/Pm8* from rye chromosome IRS, *ViRGA/Lr37/Yr17/Sr38* on chromosome 2B from *Ae. ventricosa* (McIntosh et al. 1995a, b ; Seah et al. 2001), *Lr57/Yr40* on chromosome 5D from *Ae. geniculata* (Kurupathy et al. 2007a), *Lr76/Yr70* on chromosome 5D from *Ae. umbellulata* (Bansal et al. 2015), *Sr36/Pm6* from *T. timopheevii* on chromosome 2A, *Gb2/Pm17* from *S. cereale*, and two clusters of two genes each *Lr19/Sr25* and *Sr24/Lr24* from *A. elongatum* (Sears 1956; McIntosh et al. 1991; Delibes et al. 1993; Friebe et al. 1996). These introgressed segments of major genes clusters were shown to carry diverse and multiple genes that encode nucleotide-binding and leucine-rich repeat sequences, the most common class of plant disease resistance genes (Seah et al. 2001; Mago et al. 2005a, b). R genes evolve through a variety of molecular mechanisms: point mutations, unequal crossing over, gene conversion and recombination, illegitimate recombination, and insertion/deletions all contribute to variability (Kuang et al. 2004; Michelmore and Meyers 1998). Sequence variability in R genes/alleles was mostly found in the LRR region, which was shown to play a

major role in pathogen recognition specificity (Shen et al. 2003a, b ; Yahiaoui et al. 2006 ). Tandem and segmental duplications have been reported as a source of structural plasticity of NBS-LRR genes in plant genomes. Clustering usually results from tandem duplications of paralogous sequences resulting in unequal crossing over. Analyses of the *Arabidopsis* genome indicate that numerous small-scale genomic duplications have copied or translocated one or several NBS-LRR genes from these clusters to distal and probably random locations in the genome. At some loci, tandem duplications have expanded gene families and the duplicated sequences have diverged through accumulated mutations, increasing the complexity of R gene sequences. Clusters of durable resistance genes differ from that of major genes as inactivation of *Lr34* mean inactivation of *Yr18*, *Pm38*, and *Sr57* also, while clusters of major genes *Lr26/Yr9/Sr31/Pm8* all are different loci inactivation of one cannot inactivate other (Mago et al. 2005a, b). These slow rusting genes boost the resistance of many major genes as German and Kolmer (1992) showed that *Lr34* enhance the effect of many major genes when present together. One way of prolonging the resistance of major genes is their combination with slow rusting genes. The combination of *Lr34* with *Lr12* and/or *Lr13* provided durable leaf rust resistance cultivars worldwide (Roelfs 1988). Singh and Huerta Espino (1995) showed an increased resistance of *Lr16* with the presence of slow rusting genes. Similarly, presence of slow rusting genes *Yr29* and *Yr30* increased the resistance of *Yr31* (Singh et al. 2003). Enhanced expression of major gene *Sr25* is reported in the presence of slow rusting gene *Sr2* in CIMMYT (Njau et al. 2010). The pleiotropic action of these genes on other diseases such as powdery mildew make them additionally valuable for breeding for broad spectrum resistance (Lillemo et al. 2008; Mago et al. 2011). Mostly, durable resistance genes are also found in clusters and unlike gene clusters from wild germplasm, these clusters are like single genes as described in *Lr34/Yr18/Pm38* locus.

## 12.11 Next-Generation Sequencing Technologies for Monitoring Alien Introgressions

Identification of markers closely linked with disease resistance genes has progressed in the last decade through the development of high-throughput and cost-effective genotyping facilities. One of the first high-throughput platforms in wheat, diversity arrays technology (DArT) exploits independent chip hybridization of genome representation for diversity assessment of tested genomes and could test hundreds to thousands of genomic loci in parallel (Jaccoud et al. 2001). This approach can be more efficient using high-throughput next-generation sequencing (NGS) platforms for genome sequencing referred to as genotyping-by-sequencing (GBS) and can identify several hundred thousand genome tags (Poland et al. 2012). Another approach includes the use of advances in wheat genome sequencing and



NGS technologies to develop SNP chips for wheat. All these technologies individually or in combination can be used to fine map the genes of interest.

The International Wheat Genome Sequencing Consortium (IWGSC) was established in 2005 to sequence the wheat genome to enhance the knowledge of structure and function of wheat genome and create a platform for accelerating wheat improvement. With a genome sequence in hand, breeders can have access to complete, ordered gene catalog and an almost unlimited number of molecular markers that can be used for marker-assisted selection and precision-breeding approaches (Collard and Mackill 2008; Tester and Langridge 2010). Combined strategies are being deployed by the consortium to achieve a reference genome sequence of the hexaploid bread wheat genome cultivar Chinese Spring. These include physical mapping of Chinese Spring and *Aegilops tauschii* (the D genome progenitor of bread wheat), as well as survey sequencing and BAC-based (i.e., the minimum tiling path of the physical map) reference sequencing of Chinese Spring. The physical map of *Aegilops tauschii* was completed by Jia et al. (2013). The physical map of the largest wheat chromosome (3B, ~1 Gb) was completed in 2008 (Paux et al. 2008). Physical mapping of the remaining chromosomes is underway. To facilitate anchoring, marker development, and to gain a first insight into the gene space composition, survey sequences were completed with the construction of the physical maps. The chromosome arm-based draft sequence of the bread wheat genome (IWGSC 2014) provided new insight into the structure, organization, and evolution of the large, complex genome of the world's most widely grown cereal crop. These arm-based sequences also became an immense resources for marker development. 7AL sequence was aligned against genic sequences of *Brachypodium* 7AL genic contig as well as those carrying NBS-LRR domains were identified. SSR and RGA-STS marker were developed from these contigs and mapped on 7AL of *T. boeoticum*/*T. monococcum* RIL population leading to fine mapping of two powdery mildew-resistant genes *PmTb7AL.1* and *PmTb7AL.2* (Chhuneja et al. 2015). Both the genes have been transferred to hexaploid wheat background using the linked RGA-STS marker (Elkot et al. 2015).

## 12.12 Flow Sorting of Chromosomes and Gene Identification

Dissecting and cloning individual chromosomes would largely facilitate genome analysis and gene cloning in wheat and other organisms with large and complex genomes. This approach reduces sample complexity and enables analysis at the subgenomic level. Flow cytometric chromosome sorting has been implemented successfully in many plant species, including cultivated cereals (such as bread and durum wheat), barley, rye, oats, rice, and maize (Dolezel et al. 2012). Molnár et al. (2011) reported flow sorting of individual chromosomes from *Ae. umbellulata*

( $2n = 2x = 14$ , UU) and *Ae. comosa* ( $2n = 2x = 14$ , MM) and from their natural allotetraploid hybrids (*Ae. biuncialis* and *Ae. geniculata*). This study provided opportunity for the next-generation sequencing of individual *Aegilops* chromosomes for the development of sequence-based markers and their application in wheat breeding. Tiwari et al. (2014) flow-sorted short arm of chromosome 5 Mg of *Ae. geniculata* from a wheat line in which it was maintained as a telocentric chromosome. DNA of the sorted arm was amplified, sequenced, and used for SNP discovery against wheat homoeologous group-5 assemblies. A total of 2178 unique, 5 MgS-specific SNPs were discovered. Randomly selected samples of 59 5 MgS-specific SNPs were tested and of the selected SNPs, 97 % mapped to a chromosome 5 Mg addition to wheat, and 94 % to 5Mg introgressed from a different accession of *Ae. geniculata* substituting for chromosome 5D of wheat. The validated SNPs also identified chromosome segments of 5MgS origin in a set of T5D-5Mg translocation lines; eight SNPs (25 %) mapped to TA5601 and three to TA5602, the introgression lines carrying resistance to leaf rust (*Lr57*) and stripe rust (*Yr40*) identified by Kuraparthy et al. (2007a). The development of a large number of species/genome-specific SNP markers will facilitate the precise introgression and monitoring of alien introgressions in crop-breeding programs and enable fine mapping and cloning novel genes from the wild relatives of crop plants.

### 12.13 Cloning of Alien Disease Resistance Genes

A very large number of disease-resistant genes have been mapped and molecular markers suitable for marker-assisted selection (MAS) have been identified. It was considered very difficult to clone genes from wheat as it is an allohexaploid. Some success has been achieved and some rust-resistant genes (*Lr1*, *Lr10*, *Lr21*, *Lr34*, and *Yr36*) have been cloned and characterized. *Lr21* and *Yr36* are the only alien genes which have been cloned so far.

Map-based cloning of *Yr36* was done by crossing the susceptible durum wheat variety Langdon with the resistant isogenic recombinant substitution line RSL65. A population of 4500 F<sub>2</sub> plants was screened using *Yr36* flanking markers *Xucw71* and *Xbarc136* and identified 121 lines with recombination events between these two markers. Based on genes from the rice collinear region, nine PCR markers were developed to construct a high-density map of *Yr36*. *Yr36* was mapped to a 0.14 cM interval delimited by markers *Xucw113* and *Xucw111*. BAC ends were used to rescreen the library and extend the contig by chromosome walking. BAC-end marker *Xucw127* was mapped proximal to *Yr36*, thereby completing the physical map. New markers were developed after sequencing of the BAC clones and *Yr36* resistance was mapped between *Xucw129* and *Xucw148* (0.02 cM). The gene includes a kinase and a putative START lipid-binding domain. Five independent mutations and transgenic complementations confirmed that both domains were necessary to confer resistance (Fu et al. 2009). Resequencing cloned genes can identify all mutations in single genes for population-based analyses of genetic



changes in improved gene pools. This is useful to know about the genetic impacts of modern plant breeding on specific breeding target loci.

Another alien rust-resistant gene *Lr21* was cloned by diploid/polyploid shuttle mapping strategy (Huang et al. 2003). *Lr21* spanned 4318 bp and encoded a 1080-amino-acid protein containing a conserved nucleotide-binding site (NBS) domain, 13 imperfect leucine-rich repeats (LRRs), and a unique 151-amino-acid sequence missing from known NBS-LRR proteins at the N terminus. Fine-structure genetic analysis at the *Lr21* locus detected a non-crossover (recombination without exchange of flanking markers) within a 1415-bp region resulting from either a gene conversion tract of at least 191 bp or a double crossover. With the advancements in the wheat genome sequencing and flow sorting of the chromosomes, it will become comparatively easier to clone disease-resistant genes in wheat.

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