

Chapter 10

Aegilops tauschii Introgressions in Wheat

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10.1 Introduction

Progenitor species that contributed the constituent triple genomes, designated AA, BB and DD found in the allohexaploid genome of common wheat (*Triticum aestivum*) have to a large extent been defined. *Aegilops tauschii* has been established as the D genome donor to common wheat (Kihara 1944; McFadden and Sears 1946). In contrast to the narrow geographic distribution of the other progenitor species, *Ae. tauschii* extends over a wide geographic range from eastern Turkey to China. Early taxonomic classifications based on spike morphology placed *Ae. tauschii* into two subspecies-ssp *tauschii* and ssp. *strangulata* (Eig 1929). Under subspecies *tauschii*, there were three varietal taxa classified as *anathera*, *meyeri* and *typica* whereas in subspecies *strangulata* a monotypic varietal taxa also referred

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to as *strangulata* was adopted. Some of the early studies in comparative D genomes of common wheat and accessions of the diploid progenitor led to an overly simplified conclusion that the *strangulata* taxa was the source of the D genome in the allohexaploid.

With increasing advances in genotyping, from AFLP analysis to single nucleotide polymorphisms (SNPs) where thousands of genes and DNA fragments across the entire D genome have been analysed, it has become evident that the morphological classification is inadequate in describing the specific source of the wheat D genome. A genetic classification that surpasses the morphological groupings revealed two lineages of the *Ae. tauschii* genepool, designated lineage 1(L1) and lineage 2 (L2) (Mizuno et al. 2010; Wang et al. 2013). While the evolutionary lineage classifications has some parallels with the morphological groupings, L2 contains the taxa *strangulata*, *meyeri* and some accessions of *anathera* and *typica*. These two lineages are further subdivided with sublineage 1W located in eastern Turkey, Armenia, Azerbaijan, and western Iran and sublineage 1E was distributed from central Iran to China. Sublineage 2W was found in Armenia and Azerbaijan, and sublineage 2E was located in Caspian Azerbaijan and Caspian Iran (Wang et al. 2013). On the basis of the SNP data, a population within L2E in the southwestern and southern Caspian was shown to be the main source of the wheat D genome, whereas L1 contributed as little as 0.8 % of the wheat D genome (summarized in Fig. 10.1). It has been postulated that recurrent hybridisation and introgression between *Ae tauschii* and common wheat aided by tetraploid wheats as a bridging species may have contributed to the origin of D genome diversity in wheat.

Interest in *Ae. tauschii* introgressions stems from the observation that the diploid D genome progenitor possesses a higher genetic diversity compared to bread wheat cultivars and landraces (Reif et al. 2005). *Ae. tauschii* was used to introgress specific traits that include diverse resistance genes (Olson et al. 2013; Mandeep et al. 2010; Leonova et al. 2007; Miranda et al. 2006; Ma et al. 1993; Eastwood et al. 1994), bread-making quality (Li et al. 2012), pre-harvest sprouting tolerance (Gatford et al. 2002; Imtiaz et al. 2008), yield (Gororo et al. 2002) and also morphological characters (Watanabe et al. 2006) into breeding material and cultivars of bread wheat. Since the mid-twentieth century directed efforts at *Ae tauschii* introgressions into wheat has come from two avenues. Firstly, the more common approach of artificial hexaploid wheat synthesis that is generated by crossing tetraploid wheats with *Ae tauschii* and then doubling the triploid chromosome set by colchicine treatment or spontaneous doubling arising from unreduced gamete formation. Numerous reports on synthetic hexaploids have been reviewed by Ogonnaya et al. (2013). Secondly, the process of direct introgression which involves *Ae tauschii* crosses with bread wheat and through repeated backcrosses to recover a stable bread wheat derivative (Gill and Raupp 1987), where recombinant chromosomes between the diploid and hexaploid D genomes are produced. Introgression approaches that occur via synthetic hexaploids are not limited to the D genome but also involve the A and B genomes. With the recent whole genome shotgun sequence of the synthetic hexaploid, W7984 and derivatives from recombi-



Fig. 10.1 SNP haplotypes along wheat chromosomes 1D-7D (W) and *Aegilops tauschii* lineage1 (L1) and lineage2 (L2). The pink coloured regions are polymorphic sites whereas the monomorphic regions derived from L1 are shown in blue and L2 in green. Centromeric regions are marked in red and putative haplotypes from L1 introgressed into wheat are marked in black. Figure taken from Wang et al. (2013)

nant inbred lines (Chapman et al. 2015), it provides opportunities to assess the effects of selected sequence characterized genomic intervals introgressed into wheat. Further refinements towards achieving introgressions specifically derived from *Ae. tauschii* are reported in the next section.

10.2 Development of Introgression Lines

As an alternative approach, wheat chromosome substitution lines carrying different chromosomes of *Ae. tauschii* were used in generating a set of well-characterized *Triticum aestivum*–*Ae. tauschii* introgression lines (Pestsova et al. 2001, 2006). Substitution lines of ‘Chinese Spring’ (‘CS’) in which single chromosomes of the D-genome had been replaced by homologous chromosomes of a synthetic wheat were developed by Law and Worland (1973). ‘Synthetic 6x’ was obtained from a cross of tetraploid emmer and the wild grass *Ae. tauschii* (*T. dicoccoides* var. *spontaneovillosum* × *Ae. squarrosa* ssp. *eusquarrosa*) (McFadden and Sears 1947), i.e. the D-genome substitution lines represent *T. aestivum*/*Ae. tauschii* replacements.

The D-genome substitution lines were backcrossed twice with 'CS'. In order to select a set of homozygous introgression lines representing the whole *Ae. tauschii* genome, 450 BC₂-plants were genotyped with microsatellite markers (Röder et al. 1998) and 60 were selected and selfed for development of homozygous lines. In total, 84 different homozygous 'CS (Synthetic 6x)' ('CS (Syn)') introgression lines were developed from BC₁ and BC₂ progenies (Pestsova et al. 2006). The advantage of this approach is that with a limited effort introgression lines with clean background can be generated; the disadvantage is that the approach is only applicable for varieties with existing chromosome substitution lines.

10.3 Utilisation of Wheat–*Ae tauschii* Chromosome Substitution Lines for Genetic Mapping

The set of 'CS (Syn)' D genome introgression lines has been used to identify chromosomal regions responsible for a range of agronomic traits including biotic and abiotic stress response. Both enhancing and detrimental effects were related to the *Ae. tauschii* segments incorporated into the bread wheat genome. Several examples are described below.

10.3.1 Yield and Related Characters

Yield associated traits including flowering time, plant height and single ear characters such as ear length, spikelet number and grain weight per ear were investigated under greenhouse (Pestsova et al. 2001) and field (Pestsova et al. 2006) conditions. Large effects were detected on the long arm of chromosome 5D due to the effect of the vernalisation response gene *Vrn-D1* (Fig. 10.2). The sensitivity of the synthetic wheat to vernalisation causes a delay in flowering time of at least 14 days. This delay in flowering was associated with an increased tillering and a higher spikelet number. The traits spike fertility (number of grains divided by the number of spikelets per ear) and grain weight per ear, however, were reduced. Two genomic regions appeared to have favourable alleles derived from the *Ae. tauschii* segment. Loci on chromosome 2DS contributed to earliness and ear length. The detected QTL coincided with the location of the photoperiodic insensitivity gene *Ppd-D1*. A second region was detected on chromosome arm 3DL. Favourable alleles from the *Ae. tauschii* introgressed segment for spikelet number per ear and grain weight per ear were present. The reason for finding only a few favourable alleles may be the rather long size of introgressions. It is also possible that beneficial alleles of *Ae. tauschii* were masked by many deleterious alleles located on the same chromosomal segment (Pestsova et al. 2006).

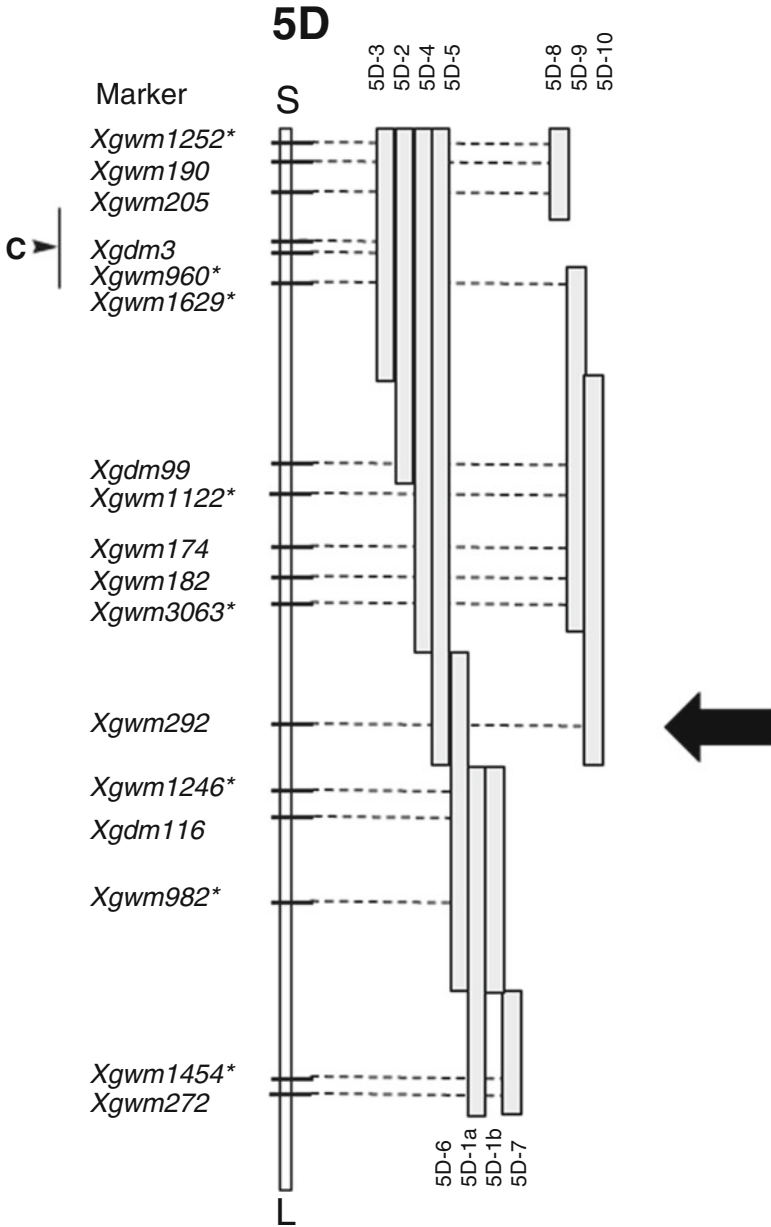


Fig. 10.2 Wheat/*Ae. tauschii* chromosome 5D introgression lines. The *black arrow* indicates the region of *Vm-D1*, showing large effects on yield-related characters. *c* centromere position, *L* long arm, *S* short arm (Pestsova et al. 2006)

10.3.2 Resistance to *Septoria Tritici Blotch* (*Mycosphaerella graminicola*)

The analysis of different sets of single chromosome substitution lines, including those derived from the ‘CS’ x ‘Synthetic 6x’ identified chromosome 7D of the synthetic wheat to carry a gene(s) encoding near complete resistance to two virulent Argentinian isolates of the foliar fungal disease septoria tritici blotch, caused by the pathogen *Mycosphaerella graminicola* (Fuckel) Schroeter in Cohn (Simón et al. 2001, 2005). In subsequent studies, Simón et al. (2007) explored the 13 chromosome 7D introgression lines, along with the parental lines ‘CS’ and ‘CS (Syn 7D)’. Both seedling and adult plant disease tests were performed by inoculation with the two isolates ‘IPO 92067’ and ‘IPO 93014’, which had been selected on the basis of prior observations made of their reactions in the ‘CS (Syn)’ single chromosome substitution lines.

Results are presented in Fig. 10.3. The introgression lines differed significantly in disease reaction from ‘CS’ in at least two (grey vertical bars) or four (black

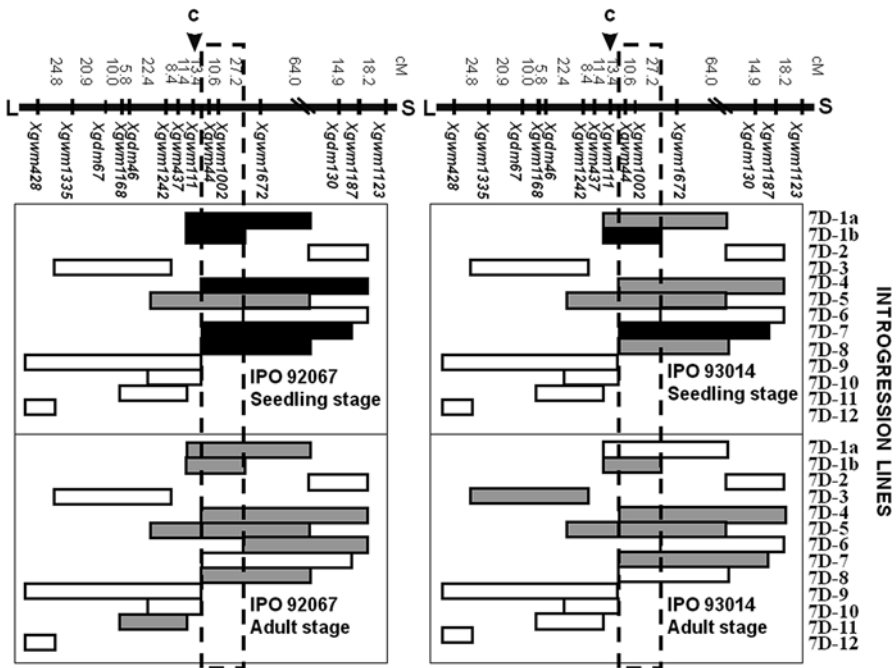


Fig. 10.3 Wheat/*Ae. tauschii* chromosome 7D introgression lines inoculated with septoria tritici blotch isolates IPO 92067 and IPO 93014 at the seedling and adult plant stages. *Lines* differing significantly from CS in two and four independent experiments are indicated by, respectively, grey and black colour. *Boxes in broken lines* indicate the position of the resistance locus. *c* centromere position, *L* long arm, *S* short arm (Simón et al. 2007)

vertical bars) independent experiments, and showed that the disease-resistance locus mapped to the centromeric region of chromosome arm 7DS. The locus identified by the 'introgression mapping' approach was consistent with that described by Arraiano et al. (2001), who investigated single chromosome recombinant lines developed from the 'CS (Syn 7D)' substitution line. The gene was designated *Stb5*. It was concluded that *Stb5* confers resistance against *M. graminicola* isolates from both Europe (Portugal, the Netherlands) and South America (Argentina).

10.3.3 Aluminium Tolerance

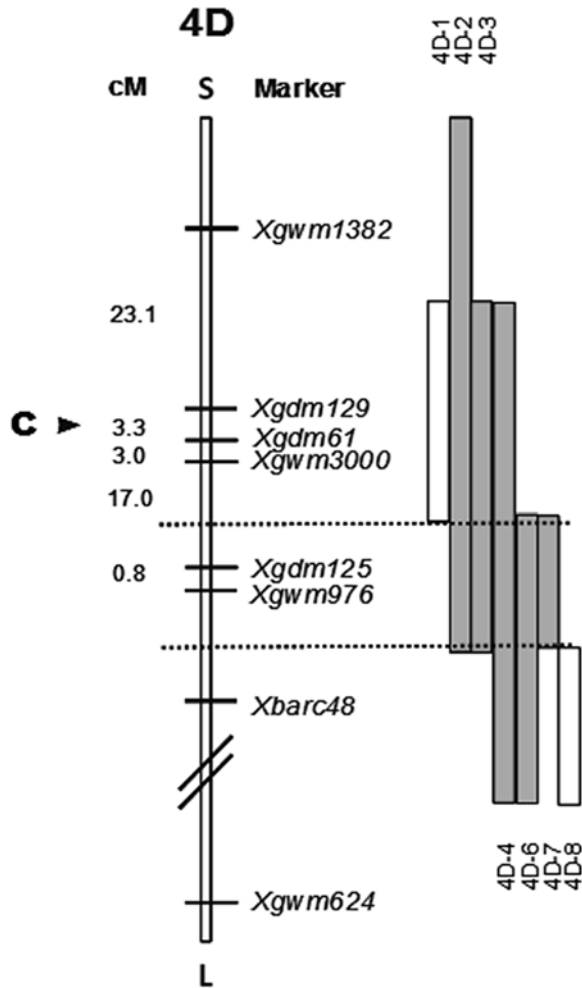
Aluminium (Al) toxicity is a major constraint to crop productivity in acidic soils. Although lime application can be used to neutralize soil acidity, and hence reduce the level of soluble Al, the development of wheat cultivars able to tolerate Al toxicity is considered a more sustainable approach. To identify loci responsible for Al tolerance Navakode et al. (2009) investigated the seven 'CS (Syn)' D genome chromosomes substitution lines as well as the 84 introgression lines. Of the whole chromosome substitution lines it was shown that 'CS (Syn 4D)' was most sensitive compared to 'CS'.

Among the 4D introgressions, lines '4D-1' and '4D-8' were tolerant, but the others were all sensitive. Genotyping of the 4D introgression lines using SSR markers enabled the delineation of the region of the 'CS' chromosome in which a gene(s) for tolerance is present (Fig. 10.4). The introgression lines derived from the remaining D genome chromosomes showed no significant deviation from control parent 'CS'. Therefore, it was concluded that the *Ae. tauschii* donor used to create the introgression lines carried no positive factors for Al tolerance. However, in a subsequent study, Ryan et al. (2010) reported identification of genetic variation for this trait in *Ae. tauschii*. A major gene for Al tolerance, *ALMT1*, located on chromosome 4DL encodes an anion channel protein which releases malate ions that bind to Al^{3+} to protect the sensitive root apex. While Al tolerance is largely determined by expression levels of *ALMT1* governed by tandem repeats in the promoter, the reported variation of Al tolerance in *Ae. tauschii* is suggested to occur outside the promoter region. The demarcated region shown in Fig. 10.4 where the *Ae. tauschii* introgressed segment has replaced CS, most likely carries the *ALMT1* gene.

10.3.4 Seed and Seedling Characters: Dormancy, Germination, Vigour and Longevity

Seed and seedling-related characters were investigated by Lohwasser et al. (2005) and Landjeva et al. (2008). For dormancy testing fresh seeds were germinated under two different temperature conditions: at 20 °C for 7 days and at 10 °C for 14 days.

Fig. 10.4 Wheat/*Ae. tauschii* chromosome 4D introgression lines investigated for AI tolerance. *White bars*: tolerant lines, *grey bars*: sensitive lines. The area within the *dotted lines* indicates the location of positive factors in ‘Chinese Spring’ and/or negative factors in *Ae. tauschii*. *c* centromere position, *L* long arm, *S* short arm (Navakode et al. 2009)



Dormancy index following Strand (1965) was calculated. One major QTL (LOD>3.0) and one minor QTL (LOD>1.5<2.0) were detected on chromosomes 6DL and 6DS, respectively (Lohwasser et al. 2005).

A comprehensive study that examined germination, seed vigour and longevity, and early seedling growth revealed QTL that mapped to chromosomes 1D, 2D, 4D, 5D, and 7D (Landjeva et al. (2008)). Most of the QTL for germination per se clustered on chromosome 1DS whereas chromosome 7DS harboured loci controlling the development of normal seedlings. Seed vigour-related QTL were present on chromosome 5DL. Loci for seed longevity were coincident with those for germination or seed vigour on chromosomes 1D or 5D. Finally, QTL for seedling growth were identified on chromosomes 4D and 5D. In summary, *Ae. tauschii* contributed

alleles allowing earlier and faster germination, whereas CS alleles were responsible for improved germination capacity, and increased synchronicity of germination. In addition, CS contributed favourable alleles for seedling growth, seed vigour and longevity.

10.4 Molecular Genetics of Disease-Resistance Gene Introgressions

Several reviews have documented the wide range of pest and disease-resistance sources found in *Ae. tauschii* and introgressed into wheat (Gill et al. 1985; Friesen et al. 2008; Halloran et al. 2008). A few of the underlying genes for these resistance sources have been cloned and many others are in the pipeline towards their eventual isolation. Two of the genes cloned, *Lr21* and *Sr33*, provide some insights into the loci found in their respective introgressed segments. *Lr21* introgressions into wheat has come from different avenues; these include direct crosses that involved the accessions TA1649 into the background of the cultivar Wichita in the United States, the use of the synthetic hexaploid RL5406 (Tetra Canthatch x *Ae. tauschii* RL5289) crossed into Canadian and Australian wheats. *Lr21* encodes a nucleotide-binding leucine rich repeat (NB-LRR) protein (Huang et al. 2003), and analysis of the corresponding locus in common wheat revealed sequence variants that included SNPs and insertion/deletion events that account for at least ten haplotypes (Fu et al. 2010). Apart from the haplotype that characterizes *Lr21* resistance, it was unclear whether the other haplotypes carried functional alleles. Nevertheless intragenic recombination involving non-functional haplotypes that reconstituted a functional *Lr21* haplotype was reported in a single plant selection from over 5000 F₂ progeny (Huang et al. 2009).

A stem rust-resistance gene, *Sr45*, was also present on the same chromosome arm (1DS) that harboured *Lr21* in the *Ae. tauschii* accession RL5289. Using the single chromosome substitution line where chromosome 1D from RL5289 had replaced the corresponding homologue in Chinese Spring (CS), the progeny from CS × CS (1DRL5289) enabled a high resolution mapping of the *Sr45* locus. By combining diagnostic markers for *Sr45* and *Lr21*, it became evident that selections from backcross derivatives between RL5406 and Australian wheats carried different *Ae. tauschii* introgressed segments; some had segments with both *Lr21* and *Sr45* while some had retained only the *Sr45* carrying segment (Periyannan et al. 2014).

Another Chinese Spring chromosome 1D substitution line from the synthetic hexaploid RL5405 (Tetra-Canthatch x *Ae. tauschii* RL5288), the source of *Sr33*, was used to generate an EMS mutagenized population to inactivate *Sr33*. These mutants were pivotal in validating the candidate *Sr33*-resistance gene from a cluster of the *Mla* (barley powdery mildew-resistance gene family)-related gene sequences at the *Sr33* locus (Periyannan et al. 2013). In addition to the *Mla* gene family, the

Sr33 locus carried an NB-LRR gene with an unusual C terminal domain that possessed an exocyst70 subunit (NB-LRR-Exo70). There is increasing evidence that adjacent pairs of distantly related NB-LRR genes where often one member within the pair with additional domains are all required for functional activity in defense against pathogens (see review by Cesari et al. 2014). While *Sr33* was confirmed to be the result of a functional diversification of an *Mla* gene member that recognize stem rust, further investigation is needed to establish whether NB-LRR-Exo70 is involved in defense to any other wheat pathogens other than stem rusts. The role of exocyst 70 in defense against bacterial and fungal pathogens has been reported in the model plant *Arabidopsis* (Pecenkova et al. 2011). It is also possible that genes with such unusual domain fusions occurs randomly through insertion, recombination or deletion events that facilitates the birth of new disease specificities under increased fitness from pathogens. Thus the introgressed *Sr33* segment and the corresponding locus in wheat of which Chinese Spring also carries an allelic variant of NB-LRR-Exo70 (IWGS wheat survey sequence) may provide new opportunities in deciphering the functional variability associated with this gene fusion.

10.5 Introgressions via Artificial Hexaploid Wheat Synthesis

Synthetic hexaploid wheat (SHW) that combines genes from the tetraploid wheat *Triticum turgidum* L. and wild ancestor *Ae. tauschii*, are arguably the most preferred and widely exploited wheat genetic resource as sources of new variation for the improvement of bread wheat. Breeding improvements are commonly achieved when the desirable gene from the primary SHW are introgressed into bread wheat via advanced derivatives (synthetic backcross-derived lines-SBLs) or synthetic derivatives (SYN-DER) (Table 10.1). As pointed out earlier, this approach introduces introgressed segments from the D genome of *Ae. tauschii* as well as the AB genomes of tetraploid wheat. The research focus during the past two decades were largely on characterizing primary SHW for various economic traits, and to proposing their putative usefulness in wheat breeding. However, there is now increasing trends to exploit characterized SHW through the introgression of desirable genes via SBLs for wheat improvement. Recently, Ogonnaya et al. (2013) presented a comprehensive review and analysis of research on SHW that covered the important historical landmarks on their development, characterization and exploitation in wheat improvement. The current efforts will focus on impacts of successful introgressions from SHW post Ogonnaya et al. (2013).

The largest collection of SHW in the world was developed at CIMMYT during 1988 to 2010 with 1300 SHW produced using about 50 improved durum genotypes and 900 *Ae. tauschii* accessions. What remains unclear is how many of these *Ae. tauschii* accessions are unique, given that the same accession can have different identification tags from the germplasm banks where they were sourced. Of these, about 100 SHW were developed using wild accessions of *Triticum dicoccoides* and *Ae. tauschii*. Additional collections of SHW were also developed at CIMMYT and

Table 10.1 Selected examples of recent advances in the characterization, and exploitation of *Ae. tauschii*, SHW and SYN-DER

Group	Trait	Germplasm	Genotyping	Phenotyping	Summary	Reference
Biotic stresses	Stem rust	456 <i>Ae. tauschii</i> accessions	–	UG-99 races	12 accessions resistant to all Ug-99 races	Rouse et al. (2011)
	Stem rust	267 <i>Ae. tauschii</i> accessions	–	Seedling	239 resistant to local Sr races	Vikas et al. (2014)
	Yellow rust	SHW	SNP 9K	Seedling, adult (2 locations)	Nine genomic regions identified	Zegeye et al. (2014)
	Pest resistance	SHW	DArT	Field trials	26 QTLs identified for resistance to five major pests.	Joukhadar et al. (2013)
	Pest resistance	SHW	–	Field trials	15 resistant to Hessian fly, 1 resistant to Russian wheat aphid, and 21 resistant to Sunn pest	El Bouhssini et al. (2013)
	Leaf rust	267 <i>Ae. tauschii</i> accessions	–	Seedling	All resistant to local <i>Lr</i> races	Vikas et al. (2014)
	Bird cherry-oat aphid and green bug	SYN-DER RILs	GBS	Evaluations for resistance	QTL on 2DL	Crespo-Herrera et al. (2014)
Yield	Spot blotch	SYN1xOcoroni86	GBS and SSRs	Two years field screening	3 QTLs identified on 1B, 3B and 5A contributed by SYN1	Zhu et al. (2014)
	TKW	231 SHW	DArT	Grain size and weight	31 loci identified for grain size, weight and shape	Rasheed et al. (2014)
	TKW, GS	4 SYN-DER F2 populations	DArT	Grain size and weight	18 QTLs for grain size and shape identified	Okamoto et al. (2013)
	Yield	SYN-DER	–	Field trials	SYN-DER cultivars prove superior to bread wheat cultivars	Tang et al. (2014)
	Wax	210 <i>Ae. tauschii</i> and 3 SYN-DER mapping populations	Genotyping <i>Jw2</i> locus	–	–	Nishijima et al. (2014)

(continued)

Table 10.1 (continued)

Group	Trait	Germplasm	Genotyping	Phenotyping	Summary	Reference	
Abiotic	Drought	210 SYN-DER	<i>TaCwi-5D</i>	Relative water contents and field trials	2 new haplotypes identified	Khalid et al. (Unpublished)	
	Drought	F2 SYN-DER	SSR and <i>TaABA8O/HI</i>	Seedling traits	QTL on 6D	Iehisa et al. (2014b)	
	Drought	SYN-DER	–	Relative water contents	SYN-DER outperformed bread wheat cultivars	Ali et al. (2014)	
	Sprouting	SYN-DER	sequencing <i>amy1</i> gene	–	QTLs on group 6 chromosomes	Yang et al. (2014)	
	Boron	SHW	DART	Relative root length at seedling stage	3 QTLs on 1A, 4A and 5B	Emebiri and Ogbomaya (2015)	
	Boron	SHW	–	Screening at seedling and adult plant stage	17 SHW tolerant	Ilyas et al. (2015)	
	Boron	<i>Ae. tauschii</i> , SHW	sequencing <i>Bot1</i> gene	–	<i>Bot-D5</i> gene identified	Pallotta et al. (2014)	
	Heat	24 SHW	SSRs	Field trials over two years	3 tolerant and 9 medium tolerant	Sharma et al. (2014)	
	Genotyping		<i>Ae. tauschii</i>	10K	–	–	Wang et al. (2013)
			<i>Ae. tauschii</i>	30K	–	–	Iehisa et al. (2014a)
		<i>Ae. tauschii</i> , SHW	<i>Ppd-D1</i>	–	–	Jones et al. (2014)	
		SHW	<i>Rht-D1</i> , <i>Ppd-D1</i> and <i>Vrn-D1</i>	–	Modified Eco-TILLING approach to identify natural variation at D-genome	Rasheed et al. (Unpublished)	

USA using winter durum wheat and *Ae. tauschii* accessions (Hanif et al. 2014) to facilitate incorporation of desirable traits into winter wheat breeding programs. In the 1980s, L.R. Joppa developed a number of spontaneous SHW from partially fertile hybrids between ‘Langdon’ durum and different *Ae. tauschii* accessions. The advantage of the latter is that they were developed with only one durum parent thus much easier to attribute potential source of new and desirable genes. Both of these two SHW collections are globally distributed and extensively exploited in genetics and pre-breeding research. Similarly, durum wheat cv. ‘Langdon’ was also used to develop 82 SHW from 69 different *Ae. tauschii* accessions and have been widely used in Japan (Takumi et al. 2009; Kajimura et al. 2011; Nishijima et al. 2014). Recently, 86 SHW were developed by Sichuan Agriculture University, China (Lianquan Zhang, Personal communication) using 23 *Ae. tauschii* accessions and 54 accessions of tetraploids comprising of *T. dicoccon*, *T. dicoccoides* and *T. turgidum* durum accessions. The other collections include limited number of Australian SHWs developed by University of Melbourne and Department of Primary industry, Victoria. A limited number were also produced at ICARDA. In recent years, additional synthetic hexaploids have been produced at the National Institute of Agricultural Botany (NIAB) in the UK.

10.6 Impact of SHWs and SBLs

10.6.1 Biotic Stresses

There is a long history of the evaluation of *Ae. tauschii* and SHW as sources of resistance to biotic stresses and their introgressions into wheat. These have been well presented by van Ginkel and Ogbonnaya (2007) and Mujeeb-Kazi et al. (2008). In the review by Ogbonnaya et al. (2013) a comprehensive catalogue of all major genes identified in *Ae. tauschii* and SHW have been documented. In Australia, successful examples of discovery of useful genes in SHW and their transfer in elite germplasm that are now routinely used in breeding programs include cereal cyst and root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*), Fusarium crown rot (*Fusarium pseudograminearum*), yellow leaf spot, Septoria nodorum blotch (SNB, *Parastagonospora nodorum*) and Septoria tritici blotch (STB, *Zymoseptoria tritici* (syn. *Mycosphaerella graminicola*) and leaf, stem and stripe rusts. The delivery of elite germplasm with introgressed genes in adapted genetic background to Australian breeding companies has been underpinned by development and use of robust phenotyping (e.g. managed environmental facility) that maximizes gene expression, development and provision of appropriate tools such as linked and/or diagnostic molecular markers accompanied by detailed knowledge and protocols for their deployment in breeding.

The delivery to breeders of new genes identified in SHW and transferred into elite Australian adapted backgrounds, along with markers is resulting in rapid introgression into breeding populations, minimising the time needed to deploy them in commercial varieties.

The prevalence and severity of loss by wheat rusts make them one of the most important threats to wheat production and priority objective in all wheat breeding programs globally. The initial screening of 456 non-duplicated *Ae. tauschii* accession for resistance to stem rust Ug99 races was an important step for subsequent identification of novel genes and their transfer to bread wheat (Rouse et al. 2011). The results suggested that 22 % of the *Ae. tauschii* accessions screened were resistant to Ug99 races. Similarly, Vikas et al. (2014) reported the results from the screening of D-genome accessions of India for leaf and stem rust resistance and found that 90% were resistant to stem rust. Recently, Periyannan et al. (2013; 2014) identified two genes *Sr33* and *Sr45* from *Ae. tauschii* and developed diagnostic markers for use in marker assisted selection in wheat.

Resistance to stripe rust was directly evaluated in 181 primary SHWs at seedling and adult plant stages in Ethiopia using virulent Kusba/Attila isolates. The SHWs were genotyped with 9K infinium SNP array and used in GWAS to identify loci linked to stripe rust resistance (Zegeye et al. 2014). They identified nine genomic regions influencing stripe rust resistance with a novel QTL on 6DS. These results provide further stimulus to exploit resynthesized SHWs as a rich source of new stripe rust resistance that may be useful in choosing SHWs and incorporating diverse yellow rust-resistance loci into locally adapted wheat cultivars.

Spot blotch caused by *Cochliobolus sativus* (anamorph: *Bipolaris sorokiniana*) is an important disease of wheat in warmer wheat growing regions like eastern India, southeast Asia, Latin America and sub-Saharan Africa (Dubin and Duveiller 2000) and can substantially reduce yields (Sharma and Duveiller 2006). SHW have been known to be the major resistance source to spot blotch (Mujeeb-Kazi et al. 2001) that have been widely used in CIMMYT's breeding activities producing many resistant derivative lines. However, there were no published reports on mapping of resistance from SHWs. Recently, Zhu et al. (2014) identified three major loci for resistance to spot blotch and favourable alleles of these loci were contributed by the SYN-DER parent.

Wheat streak mosaic virus (WSMV) is found throughout the Great Plains of North America (Burrows et al. 2009) and throughout the world, where wheat is grown (Ellis et al. 2003). Crop losses due to WSMV ranged from a trace to 13 % in Kansas from 1976 to 2000 (Bockus et al. 2001); however, complete field losses have been reported. Unfortunately, only a single dominant resistance gene, *Wsm2* (Haley et al. 2002), and minor resistance has been found in bread wheat. There are also genes for resistance to wheat curl mite which is an alternate method to reduce the incidence of WSMV through control of the vector (Martin et al. 1984). Recently, 412 SHW were screened for WSMV and 30 were found to be resistant including 4 SHW with very high level of resistance (Rupp et al. 2014). This initial finding provides new sources of resistance to WSMV and will help identify new genes and facilitate their transfer to bread wheat.

Resistance to root lesion nematodes (RLN, *Pratylenchus neglectus* and *P. thornei*) and cereal cyst nematodes (CCN) are widely acknowledged to be economically important biotic constraints in rainfed wheat production regions of Australia, USA, China, India and several countries in West Asia and North Africa (Nicol and Rivoal 2008). GWAS was conducted using 332 SHW to identify genomic regions associated with resistance to both nematode stresses using DArT markers. Seventeen DArT marker loci were found to be significantly associated with CCN and twelve to *P. neglectus* resistance. The novel QTL on chromosomes 1D, 4D, 5B, 5D and 7D for resistance to CCN and 4A, 5B and 7B for resistance to CCN are suggested to represent new sources of genes which could be deployed in further wheat improvement against these two important root diseases of wheat (Mulki et al. 2013). Similarly, Lindsell et al. (2014) identified eight QTL associated with *P. thornei* resistance in a DH population from a cross between the synthetic-derived wheat Sokoll and an Australia wheat cultivar Krichauff. Three QTL were identified on chromosome 2B, two on chromosome 6D, and a single QTL on each of chromosomes 2A, 2D and 5D. The QTL on chromosomes 2BS and 6DS mapped to locations previously identified to be associated with *Pratylenchus* resistance. Together, the QTL on 2B (QRInt.sk-2B.1–2B.3) and 6D (QRInt.sk-6D.1 and 6D.2) explained 30 and 48 % of the genotypic variation, respectively. Flanking PCR-based markers based on SSRs and SNPs were developed for the major QTL on 2B and 6D and are being used by Australian wheat breeding entities as a cost-effective high-throughput tool for marker-assisted breeding of wheat with improved *P. thornei* resistance.

Another important finding recently reported is on the identification of resistance to Hessian fly, Russian wheat aphid, and Sunn pest (El Bouhssini et al. 2013) using SHW, which are important due to the prevalence of these pests which cause economically significant damage in many wheat producing areas. About 914 SHWs were screened for resistance to these pests; fifteen SHWs showed high levels of resistance to Hessian fly and four showed moderate resistance. A SHW derived from the cross with (*T. dicoccoides*) also showed a high level of resistance to Hessian fly. The level of resistance to RWA in SHW was considerably lower; only one SHW and one durum wheat ‘Altar 84’ exhibited a high level of resistance, while four SHW were moderately resistant. Twenty one SHWs and one durum wheat ‘Langdon’ were identified to be resistant to Sunn pest at the vegetative stage. Crosses between these potentially novel resistance sources and elite bread wheat were initiated. Genetic and genomic studies using these accessions are on-going to identify and characterize the resistance genes. This will be useful in breeding programs to develop wheat germplasm with multiple resistances to these pests. In a subsequent study, Joukhadar et al. (2013) carried out GWAS with the SHW and identified 54 DArT markers which were significantly associated with 26 different QTLs conferring resistance to five insect pests (Hessian fly (HF), Russian wheat aphid (RWA), Sunn pest (SP), wheat stem saw fly (WSSF) and cereal leaf beetle (CLB)). This was the first study to utilize GWAS to identify markers linked to many insect pest resistances. The DArT markers linked to QTLs for resistance to CLB on 7DS (wPt- 66406) and 3BL (wPt-73166) were highly significant and explained up to 33 and 43 % of the variation for resistance respectively, which is quite high,

suggesting that both are major QTLs and perhaps even major genes for CLB resistance. These QTLs are likely to be novel, being the first reported identification of QTLs on 3B and 7D for resistance to CLB in wheat.

10.6.2 Grain Yield Enhancement

Number of grains per m² and thousand kernel weight (TKW) are two important components determining grain yield. In the past four decades, improvement of grain yield has come from increased grains per m², due to the utilization of *Rht* genes in wheat breeding (Rebetzke et al. 2011). However, improvement of TKW is considered to be equally as important for further improving yield potential in various parts of world (Rasheed et al. 2014; Tang et al. 2014).

Significant variation in grain yield and its component traits have been reported for SHWs and for SBLs (summarized in Ogonnaya et al. 2013). Yield advantages of SBLs over elite cultivars of bread wheat have been reported to be as high as 30% in northern Australia and 11 % in southern Australia (Dreccer et al. 2007; Ogonnaya et al. 2007). In southern Australia, Gororo et al. (2002) found that a set of SBLs yielded similarly to their bread wheat recurrent parent in high-yielding environments, but up to 49 % more than the recurrent parent in low-yielding environments. They found that significant improvements to grain yield from one SHW were achieved through increases to the number of grain produced per m². SHW that exhibited significant variation for grain weight compared to bread wheat and TKW of up to 67 g have been reported in Mexico (Calderini and Reynolds 2000).

Cooper et al. (2012, 2013) examined the yield potential of SHWs under rain-fed field conditions over years of consecutive experiments and concluded that grain weight is the most heritable trait in SHW; even some lines with higher number of spikes and higher number of grains per spike maintained their grain size and weight. Recently, Tang et al. (2014) evaluated three SBLs and five bread wheat cultivars consecutively for 3 years under field conditions in Sichuan, China. The SBLs cultivars showed on average an 11.5 % or 951 kg ha⁻¹ yield increase compared to bread wheat cultivars. This yield gain was mainly attributed to increases in both grain number per m² (5.7 %) and TKW (5.9 %). Other superior phenotypes associated with SBLs cultivars include higher rate of above-ground dry matter accumulation in the early growth stages, better partitioning to the grain, relatively compact and erect plant type with medium and upper leaves having a mean EC45° increase of 8.4 % over the non SBL cultivars at 20 days after flowering.

In a very comprehensive study, Talbot (2011) investigated the potential of SHWs to increase the grain yield of an Australian bread wheat cultivar, Yitpi, under water stressed conditions. In the study, grain yield and its major components were measured in 27 families of BC1 synthetic-derived lines under five drought stressed environments in southern Australia. Fourteen SHWs were donor parents to SBLs families with significantly ($P < 0.05$) higher grain yields compared to the recurrent Australian bread wheat Yitpi parent. These lines produced the highest

significant grain yield improvements under the lowest grain-yielding environments. The grain yield component responsible for these increases was grain weight under the highest-yielding environments, whereas grain per m² was commonly responsible under the lowest-yielding environments. The study showed that many, but not all SHWs can be used to increase the grain yield of an Australian bread wheat cultivar, particularly in low-yielding moisture-limiting environments of southern Australia.

Similarly, the yield performance of SBLs against the recurrent parent, Cham-6 and other reputed high-yielding cultivars, including Attila-7 and Wyalkatchem was conducted in nine site year by location in Mediterranean environment of Syria and Lebanon. Five SBLs had superior average yield compared to the best check, Wyalkatchem, and seventeen SBLs had superior average yield compared to the parent, Cham6. Further, two SBLs were also the first two winning genotypes in most of the nine environments using AMMI model (results not shown). The coefficient of variation (CV) from Francis and Kannenberg (1978) was used to assess a genotype stability by plotting the CV-FK against mean grain yield. The result indicated that some SBLs (e.g. 69, 9, 66, 8, 9, etc) not only possessed higher grain yield but were also stable across environments (Fig. 10.5). The grain yield was positively associated with the number of kernel per meter square, harvest index, early ground cover and vigour, and NDVI at the beginning of grain filling. The increase in grain yield was mainly attributed to two components, number of grains per m² and TKW.

Recently, Trethowan (2014) reviewed the contributions of wheat genetic resources for drought tolerance and concluded that 30 % yield advantage is associated with SHWs under drought stress. Perhaps, yield advantages in SHW are due to favourable alleles underpinning important yield related traits that are preferentially retained in SBLs (McIntyre et al. 2014). Similar results were also reported by Ali et al. (2014) which demonstrated the superiority of SBLs, over improved bread wheat cultivars. Nishijima et al. (2014) reported on sequence polymorphism of *Iw2* gene controlling glaucous appearance in *Ae. tauschii* and SBLs segregating populations. Glaucous appearance is associated with drought tolerance, prevents non-stomatal water loss, inhibits organ fusion during development, protects from UV radiation damage, and imposes a physical barrier against pathogenic infection. However, application of this information in practical wheat improvement is yet to be evaluated.

Collectively, kernel size, shape and TKW are relatively new yield-related traits that can be targeted to get more genetic gains for grain yield, following the example of yield advantages achieved in rice by enhancing kernel size (Gegas et al. 2010). Rasheed et al. (2014) conducted a GWAS for grain size, shape and TKW in a collection of SHW and identified two important loci on 3D and 6D chromosomes consistently associated with kernel length, width and TKW. Similarly, Okamoto et al. (2013) and Williams and Sorrells (2014) conducted QTL mapping in populations derived from SHW and identified several loci that underpin these traits and may have an impact on enhancing grain yield without compromising the number of grains m².

10.6.3 Impact on Providing Protection from Abiotic Stresses

Drought, heat and salinity are the major abiotic stresses that affect wheat production worldwide. Other important stresses include freezing tolerance (reproductive and vegetative), and soil toxicities including boron toxicity. The use of SHWs is seen as important genetic resources in identifying superior traits associated with some tolerance to these abiotic stresses. Salinity is a severe problem, affecting more than 800 million hectares of land worldwide that accounts for more than 6% of the global land mass (Munns and Tester 2008). It is well known that hexaploid bread wheat generally shows higher salt tolerance than its tetraploid progenitor, *Triticum turgidum*. We evaluated Na⁺ exclusion in a set of 150 genotypes including SHWs, elite ICARDA germplasm and focused identification of germplasm strategy (FIGs) genotypes. Amongst the SHWs, genotypes significantly varied in Na⁺ blade concentrations from 56 to 1216 $\mu\text{mol Na}^+ \text{g}^{-1}$ leaf blade dry weight (BDW) (exceeding 21-fold) for Aus-34453 and SHW-860 respectively. The differences between the lowest nine genotypes in term of Na⁺ blade conc. and the standard salt-tolerant Indian genotype (KHARCHIA 65 = 166 $\mu\text{mol Na}^+ \text{g}^{-1}$ BDW) were significant, and approximated threefold. This is similar to earlier results reported by Dreccer et al. (2004) who observed a threefold range of Na⁺ concentrations in SHW compared to hexaploid wheat control used in the study. Ogbonnaya et al. (2013) demonstrated the successful transfer of salinity tolerance in SHW measured as Na⁺ exclusion into an elite Australian common wheat cultivar, Yitpi with some of the SBLs showing significantly enhanced Na⁺ exclusion compared to either the SHW or the recurrent common wheat cultivar (Fig. 10.6). This was also confirmed by an independent study where the SBL genotype ranked 3rd out of 150 lines evaluated for salinity tolerance using a hydroponic system at ICARDA.

Boron toxicity is a major problem in many parts of world, especially in Australia, limiting wheat production. Previously, a major locus *Bo1* on chromosome 7BL was identified to be contributing tolerance to boron toxicity. Dreccer et al. (2003) reported high levels of B tolerance in SHWs. Tolerance to boron toxicity was also evaluated in 45 SHW derived from the susceptible durum cultivar 'Decoy' and 16 SHW were identified as tolerant which may be derived from the *Ae. tauschii* D-genome given the susceptibility of the durum parent used in the study (Ilyas et al. 2015). In a recent study, Emebiri and Ogbonnaya (2015) used a genome-wide scan with DArT markers to identify regions that might harbour novel genetic loci that confer enhanced boron tolerance in SHWs than currently available in bread wheat. They showed that the SHWs were uniformly more tolerant to boron toxicity than the sensitive check, Meering, and 25 showed tolerance levels that were superior ($P \leq 0.05$) to that of Halberd, the most tolerant wheat check cultivar. At a threshold of $-\log(P) \geq 2.8$, a mixed linear model association mapping identified DArT markers on chromosomes 1A, 4A and 5B, but only the 4A region is known to harbour genes for boron toxicity tolerance. The chromosomes 1A and 5B loci represent novel regions, which when validated will increase the options of achieving tolerance beyond that conferred by *Bo1* and *Bo4* in breeding programs.

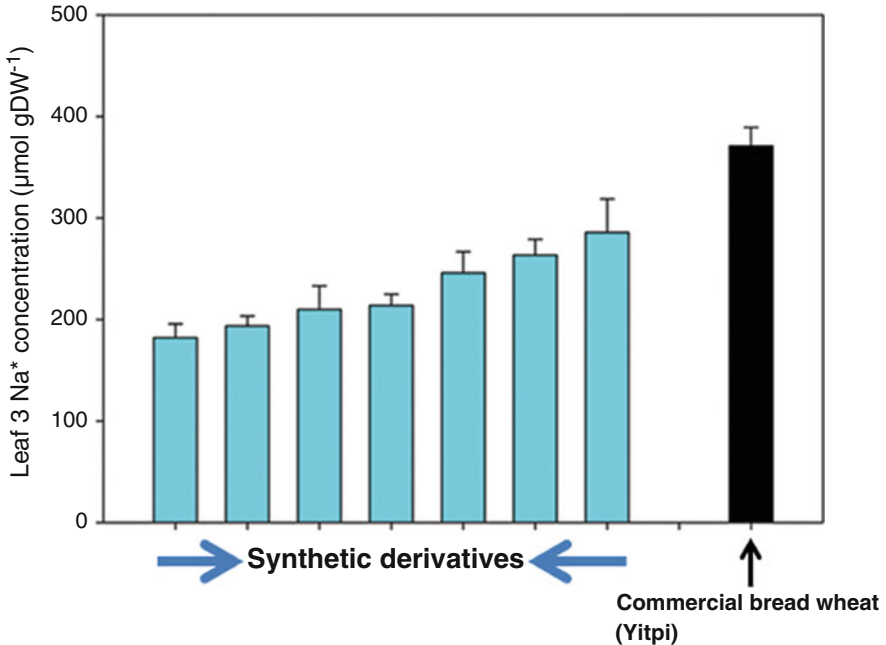


Fig. 10.6 Synthetic backcross-derived lines with lower Na⁺ exclusion than the recurrent elite Australian wheat cultivar, “Yitpi” from Ogbonnaya et al. 2013

In most of winter wheat producing area, susceptibility to freezing is an important production-limiting factor. Pearce et al. (2013) screened ten SHW and identified only one accession having nine-gene deletion at a major cold tolerance locus *Fr-B2*. The deletion is associated with freezing susceptibility and was contributed by the durum parent ‘Altar-84’ of the SHW. Winter wheat breeding programs interested in using SHW and improving freezing tolerance may benefit from preliminary screening of SHW accessions for those that do not carry deletions at the *Fr-B2* locus.

Alpha-amylase (α -Amylase-amy1) gene plays a key role in seed germination and its activity determines levels of starch degradation, seed germination, and pre-harvest sprouting (PHS), which is a serious problem in wheat production. Yang et al. (2014) isolated and characterized high α -Amylase coding genes from the wheat cultivar Chuanmai32 (PHS susceptible) and the synthetic wheat SHW-L1 (PHS resistant). Expression profiling of amy1 indicated that mRNA transcript accumulation began at a late stage of grain development. amy1 transcript accumulation in Chuanmai32 was 4.32- and 18.36-fold higher than observed in SHW-L1 at DPA25 and DPA30, respectively. Two significant expression quantitative trait loci (eQTLs) on chromosome 1BS and one on 3DS were characterized by expression analysis of amy1 transcripts and genetic analysis of SHW-L1/Chuanmai32-derived

recombinant inbred lines. The genes that encoded high PI amylase were located near the centromere on chromosomes 6AL/6BL/6DL. These results suggest that these eQTL regions may provide candidate genes that play potential roles in regulating PHS through effects on amy1 expression, and points to the possible use of SHW to improve PHS tolerance. This result is consistent with the finding of Imtiaz et al. (2008) who reported that the enhanced expression of PHS resistance in SBLs led to the development of white PHS-resistant wheat germplasm from red-grained *Ae. tauschii* accession.

Besides their use as sources of genes for improving abiotic and biotic stresses, several wheat cultivars have been released that are derived from SHWs. These include Lalma and KT-2010 in Pakistan (CIMMYT Wheat Atlas), Maravilla in Mexico (CIMMYT Wheat Atlas), Carmona in Spain (van Ginkel and Ogonnaya 2007) and Chuanmai-42 and its derivatives in China. Recently, Li et al. (2014) reviewed the current status of synthetic-derived wheat cultivars released in Southwestern China. They reported that 16 commercial wheat varieties including Chuanmai 28, 42, 43 and 47 have been released from using SHW. Apart from released cultivars, a significant proportion of international bread wheat screening nurseries by CIMMYT and ICARDA comprises of synthetic-derived germplasm which are distributed on annual basis worldwide.

10.7 International Initiatives

Several large investments are being made by the British (Wheat LOLA project), French (BREEDWHEAT) and Mexican government (SeeD) on the characterisation and utilisation of wild relatives for wheat improvement. A major component of these initiatives involves the use of synthetics including the development of introgression lines. The SeeD used more than 100 SHW in the development of Linked-Top-Cross (LTP) populations. The TC1F5 (~5000 derived lines) are currently being evaluated at Obregon under drought and heat stresses. In UK, a project was funded to introduce novel genetic variation from wheat progenitor species (*Ae. tauschii*) via SHW. Genetic diversity from 50 SHWs was backcrossed into Paragon and Xi-19 to produce over 5600 BC1-derived lines for field selection. In China, breeders began to cross CIMMYT SHWs with their local varieties in the mid-1990s, and released their first SHW-derived variety in 2003, which yielded over 20 % more than checks in provincial trials. SBLs are now reported to be grown on over five million hectares in China, some 25 % of the wheat acreage. The Synthetic Evaluation Project was funded by the Grain Research and Development Corporation (GRDC), Australia from 2001 to 2007 to improve the productivity and sustainability of rainfed wheat production in the Mediterranean environments of Australia. The project aimed to identify sources of disease resistance and abiotic stress tolerance in SHW and to incorporate them into Australian adapted germplasm.

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