

## OFFERED REVIEW

## SYNTHETIC HEXAPLOID LINES ARE VALUABLE RESOURCES FOR BIOTIC STRESS RESISTANCE IN WHEAT IMPROVEMENT

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## SUMMARY

Synthetic hexaploid wheats (SHW) are products of crosses involving tetraploid cultivars (*Triticum turgidum*, 2n=28, AABB) and diploid goat grass (*Aegilops tauschii*, 2n=14, DD), followed by chromosome doubling of F<sub>1</sub> hybrids. They are genomically amphidiploids (2n=42, AABBDD), combining the genomes of their parents. SHW exhibit resistance to some biotic factors, mainly fungi and insects, and may serve as valuable resources in wheat breeding. They can be involved in backcrosses with elite bread wheat cultivars to produce lines with superior quality, disease resistance and yield. In this review, we summarize the published data for biotic stress resistance in synthetic wheats and the potential use of synthetic-derived backcrossed lines in bread and durum wheat breeding. The exotic genes, controlling important biological traits in SHW produced so far, should contribute to the development of new wheat varieties.

*Key words:* *Triticum* species, *Aegilops tauschii*, synthetic wheat, biotic stresses, resistance.

## INTRODUCTION

Synthetic hexaploid wheats are obtained from crosses between the tetraploid wheat *Triticum turgidum* L. (genome AABB, 2n=28) and the wild relative *Aegilops tauschii* Coss. (genome DD, 2n=14, synonyms: *Aegilops squarrosa*, *Triticum tauschii*) followed by chromosome doubling to establish a hexaploid with A, B and D genomes (Trethowan and van Ginkel, 2009). About 0.5 million years ago the cross between *Triticum urartu* and a close relative of *Aegilops speltoides* resulted in *T. turgidum* ssp. *dicoccoides* (wild emmer). Later, the domesticated form of this species, *T. turgidum* ssp. *dicoccon* (cultivated emmer) intercrossed with *Ae. tauschii*

(goat grass) originating *Triticum aestivum* (hexaploid bread wheat). It is believed that only a few accessions of the female parent were involved in the evolution of common wheat (Ogbonnaya *et al.*, 2005). Hence, the genetic diversity of bread wheat was largely reduced, as compared with its crossing parents. This so-called evolutionary bottleneck is the reason for the narrow genetic variation present at the hexaploid level in wheat. Many genes can be introgressed into common wheat by the 'bridge' of re-synthesized hexaploid (primary synthetics) or amphidiploids, obtained from crossing the tetraploid wheat with *Ae. tauschii*, in a manner analogous to the evolution of hexaploid wheat (Zhang *et al.*, 2008). In fact, using artificial crossing between any tetraploid form (2n=28, AABB; Table 1) and goat grass (2n=14), bread wheat has been recreated or re-synthesized (Trethowan and van Ginkel, 2009).

Durum wheat was first used to transfer genes from *Ae. tauschii*, giving rise to a synthetic hexaploid (Kihara *et al.*, 1957; Tanaka, 1959, 1961). In this way, several disease and insect resistance genes were transferred from goat grass to common wheat (Kerber and Dyck, 1969; Dyck and Kerber, 1970; Joppa, 1980; Harvey *et al.*, 1980; Hatchett *et al.*, 1981). Merkle and Starks (1985) and Gill and Raupp (1987) were the first to initiate a direct genetic introgression from *Ae. tauschii* to common wheat, highlighting the breeding significance of their hybrids. Currently, over 1000 primary synthetic hexaploid wheats have been developed at the International Maize and Wheat Improvement Center (CIMMYT) and by other organizations worldwide (Mujeeb-Kazi, 2003; van Ginkel and Ogbonnaya, 2007).

Modern tetraploid durum wheat (*T. turgidum* ssp. *durum*) cultivars have been predominantly used to produce new primary synthetic wheats (Trethowan and Mujeeb-Kazi, 2008), while a few dozen combinations include *T. turgidum* ssp. *dicoccoides* and ssp. *dicoccon*. These wild tetraploid accessions have the potential to improve the stress adaptation of hexaploid wheat and represent the genetic variability available in the primary wheat gene pool. The current challenge is to identify useful resistance genes in the synthetic wheats produced and the best utilization of this new diversity for developing bread and durum wheat varieties resistant to biotic constraints.

## RESISTANCE TO BIOTIC STRESSES

**Leaf rust and stripe rust.** Resistance to fungi remains one of the major agronomic traits for wheat breeding and crop production (Friesen *et al.*, 2008; Maccaferri *et al.*, 2010). Exploiting synthetic amphiploids is an effective and rapid way of introgressing desirable traits from related species into cultivated wheats (Spetsov and Savov, 1992; Goncharov *et al.*, 2007; Plamenov *et al.*, 2009). The synthetic wheat line Syn022L, derived from the cross *T. turgidum* ssp. *dicoccoides* x *Ae. tauschii*, was used to localize main alleles (QTL) for the improvement of leaf rust resistance in an advanced backcross population. Some known resistance genes were identified, whereas others appeared to be novel resistance loci (Naz *et al.*, 2008). Two synthetic lines of the 11 SHW obtained, resisted leaf rust at the seedling stage better than the lines carrying the leaf rust resistance gene *Lr21* derived from *Ae. tauschii* (Moraes-Fernandes *et al.*, 2000) (Table 2). In particular, SHW line TA4152-60 was found to carry QTLs for adult plant leaf rust resistance in chromosome arms 3AL, 3BL and 5BL (Chu *et al.*, 2009).

Many SHW have been tested for resistance to wheat stripe rust. A great diversity in response was found among them and attributed to the A and B genomes, and/or to the goat grass D genome (Ma *et al.*, 1995; Assefa and Fehrmann, 2000; Rizwan *et al.*, 2007). Lange and Jochemsen (1992) generated 22 SHW from 11 stripe rust-resistant wild emmer accessions and eight *Ae. tauschii* accessions. However, resistance in one or both parents was frequently suppressed in the synthetic lines, indicating the presence of suppressor genes on the AB and D genomes (Kema *et al.*, 1995). According to analysis of inherited mode, resistance genes to stripe rust in synthetic wheats CI142 and CI191 were tentatively designated *YrC142* and *YrC191*, respectively (Wang *et al.*, 2009; Ren *et al.*, 2010).

**Stem rust and powdery mildew.** Marais *et al.* (1994) observed variation in stem rust resistance in a progeny from crosses involving three species, which included *T. turgidum* and *Ae. tauschii*. Moraes-Fernandes *et al.* (2000) synthesized 11 lines from crosses between durum genotypes and *Ae. tauschii* accessions, performing seven different cross combinations. Eight SHW expressed better levels of resistance to several stem rust races than *Sr33*, the gene that had been transferred earlier from *Ae. tauschii*. The resistance in these SHW lines might be derived from both parents as they were resistant to all investigated rust races. The temporarily designated resistance genes *SrTmp* (wheat origin), *SrR* and *Sr1A.1R* (rye origin), and a few other uncharacterized sources originating from re-synthesized hexaploid lines (*SrSynt*) offered further diversity (Singh *et al.*, 2008).

One hundred and twenty seven SHW produced by the CIMMYT wheat program and 144 durum geno-

types from the 39<sup>th</sup> International Durum Screening Nursery were assessed for response to Australian stem rust pathotypes differing in virulence. Synthetic hexaploids were found to carry the D-genome located genes *Sr30* and *Sr33* in addition to the genes postulated in durum wheats (Bariana *et al.*, 2009). The *Ae. tauschii*-derived gene *Sr46* could also be present in some genotypes. Some lines were thought to carry yet uncharacterized genes for stem rust resistance. The Opata/synthetic-derived mapping population was also tested and was found to segregate for *Sr9e*, *Sr13*, *Sr30* and *Sr33* genes. *Sr30* was contributed by Opata and other genes were contributed by the synthetic parent (Bariana *et al.*, 2009). New sources of resistance identified by Toor *et al.* (2009) will also be involved in the breeding process.

Expression of complete and isolate-specific resistance from *Ae. tauschii* was observed in some SHW derived from four mildew susceptible durum parents, each crossed with a set of resistant diploid accessions (Lutz *et al.*, 1994; Kong *et al.*, 1999). Synthetic amphidiploids involving different combinations of both parents generally showed a decrease in powdery mildew resistance compared with that expressed by the *Ae. tauschii* lines used in the crosses. Recently, Li *et al.* (2010) indicated *Pm-M53* to be a new powdery mildew resistance gene in synthetic wheat M53 derived from *T. durum* x *Ae. tauschii* cross (Table 2). The gene has been allocated to chromosome arm 5DL.

**Septoria diseases and scab.** *Septoria* species are important agents of wheat diseases affecting million of hectares worldwide. Some SHW have shown excellent resistance that appears to be leading towards immunity against leaf blotch caused by *Mycosphaerella graminicola* (Fuckel) J. Schröt. (Arraiano *et al.*, 2001; Ortiz *et al.*, 2008). A high level of resistance to *Stagonospora nodorum* leaf and glume blotch has also been detected among primary synthetics. From the *Ae. tauschii* genome, chromosome 5D mainly and, to a lesser extent 3D and 7D, were found to confer resistance to wheat reducing lesion cover to nearly that of the amphidiploid *T. turgidum* ssp. *dicoccon* x *Ae. tauschii* (Nicholson *et al.*, 1993; Loughman *et al.*, 2001). Many SHW have expressed high level of resistance to leaf blotch and tan spot (Friesen *et al.*, 2008; Morris *et al.*, 2010) and the synthetic hexaploid CPI133872 was reported to be a carrier of genes for resistance to *Septoria tritici* leaf blotch and yellow leaf spot (tan spot) (Zwart *et al.*, 2010).

Fusarium head blight (FHB) or scab is a most important fungal disease that affects wheat reducing kernel weight, yield and flour properties (Mujeeb-Kazi *et al.*, 2001a; Ortiz *et al.*, 2008; Buerstmayr *et al.*, 2009). *Fusarium graminearum* is the major pathogen worldwide while *F. culmorum* tends to predominate in maritime regions (Stenglein, 2009). The *Fusarium* species associated with scab produce mycotoxins that contami-

**Table 1.** Tetraploid *Triticum* species with AB-nuclear constitution (2n=28) according to van Slageren (1994) and Ortiz *et al.* (2008).

| Species classification   | Frequently used name     | Common name             |
|--|--------------------------|-------------------------|
| <i>Triticum turgidum</i> L.  |                          |                         |
| <i>Triticum turgidum</i> ssp. <i>carthbicum</i> (Nevski) A. Löve et D. Löve                | <i>T. carthbicum</i>     | Persian wheat           |
| <i>Triticum turgidum</i> ssp. <i>dicoccon</i> (Schrank) Thell.                             | <i>T. dicoccon</i>       | Emmer wheat             |
| <i>Triticum turgidum</i> ssp. <i>durum</i> (Desf.) Husn.                                   | <i>T. durum</i>          | Macaroni or durum wheat |
| <i>Triticum turgidum</i> ssp. <i>paleocolchicum</i> (Dekapr. et Menabde) Mac Key ex Hanelt | <i>T. paleocolchicum</i> |                         |
| <i>Triticum turgidum</i> ssp. <i>polonicum</i> (L.) Thell.                                 | <i>T. polonicum</i>      | Polish wheat            |
| <i>Triticum turgidum</i> ssp. <i>turanicum</i> (Jakubz.) A. Löve & D. Löve                 | <i>T. turanicum</i>      | Khorassan wheat         |
| <i>Triticum turgidum</i> ssp. <i>turgidum</i>  | <i>T. turgidum</i>       | Pollard wheat           |
| <i>Triticum turgidum</i> ssp. <i>dicocoides</i> (Körn. ex Asch. et Graebn.) Thell.         | <i>T. dicocoides</i>     | Wild emmer              |

nate the grain. Oliver *et al.* (2005) screened 31 SHW, three of which were resistant to FHB. Because the durum wheat parent involved in these lines is cv. Langdon, which is susceptible to the pathogen, the resistance of the lines might originate from the *Ae. tauschii* parent or from intergenomic gene interaction. More recently, additional sources including synthetic-derived wheat lines, exhibited moderate scab resistance (Berzonsky *et al.*, 2004; Ortiz *et al.*, 2008).

**Leaf blight and Karnal bunt.** *Cochliobolus sativus* causing spot blotch and *Pyrenophora tritici-repentis* (Died.) Drechs. inducing tan spot, are the pathogens responsible for leaf blight (Mujeeb-Kazi *et al.*, 2001b; Joshi *et al.*, 2007; Singh *et al.*, 2010). Two homozygous recessive genes (*hlbr1* and *hlbr2*) are responsible for resistance to *Bipolaris sorokiniana* (anamorph of *C. sativus*) in the synthetic wheat line Chirya-3 (Ragiba *et al.*, 2004a, 2004b), a CIMMYT synthetic line identified as highly resistant to *Helminthosporium* leaf blight disease. Linkage analysis using SSR markers detected single genes for resistance to tan spot in three SHW which are clustered on the short arm of chromosome 3D, i.e. gene *tsn3a* in line XX41, *tsn3b* in XX45 and *tsn3c* in XX110 (Cox *et al.*, 1992; Tadesse *et al.*, 2007). The linked markers and genetic relationship of these genes will greatly facilitate the use of SHW in breeding and deployment of cultivars with leaf blight resistance. Siedler *et al.* (1994) found that SHW generally show a decreased resistance to *Pyrenophora tritici-repentis*, although several lines express a higher resistance than the diploid parents. Five SHW exhibited higher resistance to tan spot than the standard resistant common wheat cultivar Red Chief. QTL analysis revealed a total of five genomic regions significantly associated with tan spot resistance (Chu *et al.*, 2008). Cruz *et al.* (2010) reported partial resistance to blast, caused by *Pyricularia grisea*, on common and synthetic wheat genotypes at the seedling and adult plant growth stages.

Karnal bunt (*Tilletia indica* Mit.) is considered a disease of moderate economic importance (Villareal *et al.*,

1994), but in Europe and Australia this fungus is suspected to be highly risky (Ortiz *et al.*, 2008). Karnal bunt resistance exhibited by SHW has been transferred into elite bread wheat cultivars susceptible to this disease (Mujeeb-Kazi *et al.*, 2006) (Table 2).

**Nematodes and insects.** Root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*) attack wheat roots reducing tillering, biomass and grain yield. In Australia, both species are widespread and damage wheat significantly (Thompson *et al.*, 1999; Zwart *et al.*, 2006). Until recently, the only source of partial resistance to *P. thornei* was the bread wheat line GS50a. However, Thompson and Haak (1997) found resistance to *P. thornei* in all taxonomic subgroups of *Ae. tauschii*. Out of 186 SHW accessions 59 (32%) proved to be more resistant to nematodes than the control, bread wheat GS50a. Five SHW lines with superior resistance to *P. thornei* showed also excellent resistance to *P. neglectus*. It was also found that SHW with only one resistant parent are not as resistant as those with both resistant parents (Zwart *et al.*, 2004). Resistance genes from both the D genome and the A and/or B genomes were contributing to resistance in the synthetic hexaploid (Vanstone *et al.*, 2008; Thompson, 2008). Latest studies showed that QTLs for resistance to *P. thornei* in the SHW occurs on chromosomes 2BS and 6DS (Zwart *et al.*, 2006; see review by Thompson *et al.*, 2008), and confirmed the polygenic nature of resistance to both nematodes.

Hollenhorst and Joppa (1983) and Lage *et al.* (2003) found high levels of resistance to greenbug (*Schizaphis graminum* Rondani) among SHW. The synthetic line Largo carried the greenbug resistance gene *Gb3*, which is different from the resistance identified in W7984, another SHW line (Weng *et al.*, 2005). This line, constructed from the cross of durum cv. Altar 84 with *Ae. tauschii*, is one of the parents of the marker-rich ITMI population, which consists of 150 recombinant inbred lines derived by single-seed descent (Sardesai *et al.*, 2005). Comparative mapping in segregation analysis us-

**Table 2.** Biotic resistance in synthetic hexaploid wheats (SHW) and major character/genes successfully transferred to synthetic backcross-derived wheat lines.

| Tetraploid species involved in SHW   | Biotic agent/trait                       | References  |
|--|--|---|
| <i>T. turgidum</i> ssp. <i>durum</i><br>( <i>T. durum</i> , <i>T. turgidum</i> ) | Stem, leaf rust and powdery mildew       | Moraes-Fernandes <i>et al.</i> (2000); Friesen <i>et al.</i> (2008) |
|  | Stem rust                                | Sehdal <i>et al.</i> (2006)   |
|  | Leaf rust                                | Chu <i>et al.</i> (2009)  |
|  | Powdery mildew                           | Lutz <i>et al.</i> (1994)   |
|  |  | Kong <i>et al.</i> (1999)   |
|  | <i>Pm-M53</i> gene                       | Li <i>et al.</i> (2010)   |
|  | Tan spot                                 | Siedler <i>et al.</i> (1994)  |
|  |  | Tadesse <i>et al.</i> (2007)  |
|  |  | Chu <i>et al.</i> (2008)  |
|  | Stripe rust                              | Rizwan <i>et al.</i> (2007)   |
|  |  | Wang <i>et al.</i> (2009)   |
|  |  | Ren <i>et al.</i> (2010)  |
|  | Tan spot and SN leaf blotch <sup>1</sup> | Xu <i>et al.</i> (2004)   |
|  |  | Friesen <i>et al.</i> (2008)  |
|  | <i>Helminthosporium</i> leaf blight      | Ragiba <i>et al.</i> (2004)   |
|  |  | Iftikhar <i>et al.</i> (2009)                                       |
|  | Root-lesion nematode                     | Zwart <i>et al.</i> (2004)  |
|  | Thompson (2008)                          |   |
| Spot blotch <sup>2,3</sup>   | Mujeeb-Kazi <i>et al.</i> (2001b)        |   |
| Karnal bunt  | Villareal <i>et al.</i> (1994)           |   |
|  | Sehdal <i>et al.</i> (2006)              |   |
| Karnal bunt <sup>3</sup>   | Mujeeb-Kazi <i>et al.</i> (2006)         |   |
| <i>Fusarium</i> head blight  | Oliver <i>et al.</i> (2005)              |   |
|  | Ortiz <i>et al.</i> (2008)               |   |
| Greenbug   | Weng <i>et al.</i> (2005)                |   |
|  | Sotelo <i>et al.</i> (2009)              |   |
| Hessian fly  | Xu <i>et al.</i> (2006)                  |   |
|  | Friesen <i>et al.</i> (2008)             |   |
| Tolerance to <i>Barley yellow dwarf virus</i>                                    | Saffdar <i>et al.</i> (2009)             |   |
| <i>T. turgidum</i> ssp. <i>dicoccon</i><br>( <i>T. dicoccum</i> )                | SN leaf blotch                           | Nicholson <i>et al.</i> (1993)                                      |
|  |  | Loughman <i>et al.</i> (2001)                                       |
|  | Russian wheat aphid                      | Lage <i>et al.</i> (2004)   |
|  | Greenbug                                 | Lage <i>et al.</i> (2003)   |
| <i>T. turgidum</i> ssp. <i>dicoccoides</i>                                       | Suppression of stripe rust resistance    | Kema <i>et al.</i> (1995)   |
|  | ST leaf blotch <sup>4</sup>              | Arraiano <i>et al.</i> (2001)                                       |
|  |  | Adhikari <i>et al.</i> (2003)                                       |
|  | Leaf rust <sup>3</sup>                   | Naz <i>et al.</i> (2008)  |
|  | <i>Fusarium</i> head blight              | Berzonsky <i>et al.</i> (2004)                                      |

<sup>1</sup>, SN leaf blotch=*Stagonospora nodorum* leaf blotch caused by *Phaeosphaeria nodorum*, anamorph *Septoria* (*Stagonospora*) *nodorum*;

<sup>2</sup>, Spot blotch caused by *Cochliobolus sativus*, anamorph *Bipolaris sorokiniana*;

<sup>3</sup>, Character/gene transferred to synthetic derived wheat lines;

<sup>4</sup>, ST leaf blotch=*Septoria tritici* leaf blotch caused by *Mycosphaerella graminicola*, anamorph *Septoria tritici*.

ing a set of microsatellite markers provided further evidence that greenbug resistance in W7984 and Largo is conditioned by two different loci. The resistance gene in the first line is designated *Gb7*.

The currently identified resistance genes to the Russian wheat aphid (RWA) (*Dn1-Dn9* and *Dnx*) are from *Aegilops tauschii*, rye and wheat (Bouhssini *et al.*, 2011).

Fifty-eight SHW involving *T. turgidum* ssp. *dicoccon* in the pedigree, were evaluated for resistance to RWA under field conditions. Resistance levels were slightly below that found in tetraploid parents, but no resistance suppression was observed among the tested materials. Thus, the resistance detected in SHW may differ from that expressed by previously identified RWA-resistant

genes (Lage *et al.*, 2004).

Hessian fly (HF) (*Mayetiola destructor* Say) is a major pest of wheat in North Africa, Europe, North America and, partly in Asia (Tyler and Hatchett, 1983; Friesen *et al.*, 2008). Resistance to the Syrian HF biotype, was found in 28 *Aegilops* accessions and expressed in four SHW lines. These sources of resistance are being used in ICARDA wheat breeding programs for the development of HF resistant germplasm (Bouhssini *et al.*, 2008). One gene (*H32*) conferring resistance to HF was identified in the synthetic W7984 (Sardesai *et al.*, 2005).

**Viruses.** There is genetic variation for virus tolerance in wheat (Trottet and Gouis, 2004; Bass *et al.*, 2006; Benkovics *et al.*, 2010) in which, as in oat, tolerance may be multigenic (Ayala *et al.*, 2002). Among viruses, *Barley yellow dwarf virus* (BYDV) is very common and destructive on many cereals including durum and bread wheats. True resistance to this virus has not been found in the *Aegilops-Triticum* group. Although resistance genes were identified in more than 10 wild relative species belonging to different genera of *Poaceae* (Zhang *et al.*, 2009), information on SHW as carriers of virus tolerance or resistance is scant. Recently, Saffdar (2007) evaluated Elite II SHW against BYDV and found some to express virus tolerance. RAPD analysis revealed high levels of genetic diversity in these synthetic wheats, suggesting that some of them could be potential sources for wheat improvement (Saffdar *et al.*, 2009).

## GENETIC BASIS FOR RESISTANCE TO BIOTIC STRESSES

Fungi detrimental to wheat are controlled by race-specific and race-nonspecific genes. Much of the race-specific or major gene resistances have been overcome with time by new virulent races of the pathogens. SHW express major and adult-plant (or race-nonspecific) resistance to almost all fungal pathogens (Table 3). There are nine named leaf rust resistance genes mapped in the D genome of wheat and many *Ae. tauschii* accessions contain more than one resistance gene (Gill *et al.*, 2008). Innes and Kerber (1994) identified three different adult-plant resistance genes in three synthetic wheats based on different accessions of *Ae. tauschii* from Iran. Expression of resistance is affected by environment as well as genetic background.

Thirty one and 14 genes for stripe rust resistance are localized in the B and D genomes, respectively (Chen, 2005). In addition, three new genes were discovered in SHW, tentatively designated as *YrC142*, *YrCH42* and *YrC191* (Table 3). Two SSR markers distinguish *Yr10*, *Yr15*, *Yr24* and *Yr26* from *YrC142* which derives from the synthetic CI142 and, most likely, is a new gene or a new allele at the *Yr26* locus (Wang *et al.*, 2009). The

new genes (*YrC142*, *YrCH42* and *YrC191*) are localized in chromosome 1B. Seedling resistance was reported in synthetic hexaploids indicating the presence of major genes for stripe rust resistance. Some susceptible to stripe rust SHW seedlings displayed adult-plant resistance exhibiting the presence of potentially novel race-nonspecific genes for further exploitation. QTLs for stripe rust resistance were found in B and D genomes of synthetic wheats.

More than 40 genes for stem rust resistance have been identified, only 20 of which originating from hexaploid bread wheat (Leonard and Szabo, 2005). Five major resistance genes, most often inherited in a qualitative manner, are present in SHWs (Table 3). Because stem rust populations have the potential for virulence shifts, it is important that novel resistance genes be identified and transferred to wheat. The causal stem rust race, known as Ug99 (TTKSK), carries virulence for several fungal resistance genes present in wheat cultivars. Some level of resistance to that race was observed in synthetic-derived wheat backcrossed (SDWB) lines (Singh *et al.*, 2006). It is supposed that the resistance in SDWB lines (Nos. 6070, 6071, 6107 and 6108) is governed by genes *Sr13* and *Sr14* on chromosomes 6AL and 1BL, respectively, originating from durum wheat, and by *Sr33* and *Sr45* on chromosomes 1DL and 2DS, respectively, deriving from *Ae. tauschii* (Njau *et al.*, 2010; Table 3). The first three genes (*Sr13* and *Sr14* and *Sr33*) confer only moderate levels of resistance (Jin *et al.*, 2007), whereas the response of *Sr45* to Ug99 rust race at the seedling stage and under field conditions is yet to be determined.

Resistance to powdery mildew has been associated with D-genome chromosomes. New dominant gene, temporarily designated as *Pm-M53* in 5DL, was reported in the Mexican line M53, developed at CIMMYT from the cross between *T. durum* and *Ae. tauschii* 249 (Li *et al.*, 2010; Table 3). Up to now, more than 55 powdery mildew-resistant alleles have been identified at 43 loci (*Pm1* to *Pm43*). Eight genes mediating resistance to powdery mildew have been mapped on the D genome, four of them (*Pm2*, *Pm19*, *Pm34* and *Pm35*) originating from *Ae. tauschii*.

Nicholson *et al.* (1993) determined the location of resistance to *S. nodorum* (SNB), in a SHW developed from *T. turgidum* ssp. *dicoccon* and concluded that the resistance was associated with three chromosomes from D genome. Disease expression was dependent on the specific tetraploid x *Ae. tauschii* combination. SNB resistance was shown to be under polygenic control (Kim *et al.*, 2004). A gene *Snn1*, located in chromosome 1BS, is a host gene conferring sensitivity to SnTox1, a toxin that was partially purified from an isolate Sn2000 of *S. nodorum* (Liu *et al.*, 2004). The inheritance of resistance to SNB in wheat has been reported as being qualitative, but more often as quantitative in nature.

Eight genes (*Stb1-8*) for resistance to *Septoria tritici*

**Table 3.** Major genes and QTLs for resistance to biotic stresses in synthetic hexaploid wheats.

| Biotic agent   | Gene designation   | Chromosome localisation   | SHW/parents   | Reference  |
|--|--|---|---|--|
| Leaf rust ( <i>Puccinia triticina</i> )  | <i>ALrA, ALrB, ALrC</i>  | QTLs in 3AL, 3BL, 5BL and 6BL<br>QTL in 3DL<br>QTL in 1D                                | TA4152-60/ND495<br>CPI133872/Janz<br>Batis/Syn022L<br>RL5865, RL5866, RL5867                                  | Chu <i>et al.</i> (2009)<br>Zwart <i>et al.</i> (2010)<br>Naz <i>et al.</i> (2008)<br>Innes and Kerber (1994)                      |
| Stripe rust ( <i>Puccinia striiformis</i> )  | <i>YrC191</i><br><i>YrCH42</i><br><i>YrC142</i>                      | 1BS<br>1B<br>1B<br>QTLs in 3DL, 1BL, 4BL and 7DS  | CPI/Gediz/3/Goo//Jo69CRA/4/ <i>Ae.sq629</i><br>CI142 (Garza/Boy// <i>Ae. squarrosa</i> 271)<br>CPI133872/Janz | Ren <i>et al.</i> (2010)<br>Li <i>et al.</i> (2006)<br>Wang <i>et al.</i> (2009)<br>Zwart <i>et al.</i> (2010)                     |
| Stem rust ( <i>Puccinia graminis</i> )   | <i>Sr8b, Sr9e, Sr30</i> and <i>Sr33, Sr46</i>                        | <i>Sr9e</i> -2BL, <i>Sr30</i> -5DL, <i>Sr33</i> and <i>Sr46</i> -D-genome<br>QTL in 3DL | Opata M85/Synthetic W7984 <sup>1</sup><br>CPI133872/Janz  | McIntosh <i>et al.</i> (2008) Bariana <i>et al.</i> (2009)<br>Zwart <i>et al.</i> (2010)   |
| Race Ug99 (TTKSK)  | <i>Sr13, Sr14, Sr33</i>  | 6AL, 1BL, 1DL   | Nos. 6070, 6071, 6107, 6108   | Njau <i>et al.</i> (2010)  |
| Powdery mildew ( <i>Blumeria graminis</i> )  | <i>Pm-M53</i>  | 5D, 7D<br>5DL   | Mexican M53   | Lutz <i>et al.</i> (1994)<br>Li <i>et al.</i> (2010)   |
| Septoria diseases  |  |   |   |  |
| Leaf blotch ( <i>Mycosphaerella graminicola</i> )  | <i>Stb8</i><br><i>Stb5</i>   | QTL in 3DL<br>7BL<br>7DS<br>3D, 5D and 7D   | CPI133872/Janz<br>Opata M85/Synthetic W7984<br>Synthetic 6x<br><i>T. dicoccum</i> x <i>Ae. squarrosa</i>      | Zwart <i>et al.</i> (2010)<br>Adhikari <i>et al.</i> (2003)<br>Arraiano <i>et al.</i> (2001)<br>Nicholson <i>et al.</i> (1993)     |
| <i>Stagonospora nodorum</i>  | <i>Snn1</i> <sup>2</sup>   | 1BS   | Opata M85/Synthetic W7984   | Liu <i>et al.</i> (2004)   |
| Scab ( <i>Fusarium</i> head blight)  |  | QTL in 3AS  | 01NDSWG-5   | Hartel <i>et al.</i> (2004)  |
| <i>Helminthosporium</i> leaf blight<br>Yellow leaf spot (tan spot) ( <i>Pyrenophora tritici-repentis</i> ) | <i>hlbr1</i> and <i>hlbr2</i><br><br><i>tsr3, Tsn3b, tsn3c, tsr4</i> | 7B and 7D<br>QTLs in 3DL, 5AS and 5BL<br><br>QTLs in 2AS, 4AL, 5AL and 5BL<br>3DS, 3A   | Chirya-3<br>CPI133872/Janz<br><br>TA4152-60/ND495<br>SHW XX41, XX45 and XX110                                 | Ragiba <i>et al.</i> (2004a,b)<br>Zwart <i>et al.</i> (2010)<br><br>Chu <i>et al.</i> (2008)<br>Tadesse <i>et al.</i> (2007, 2010) |
| Nematodes  |  |   |   |  |
| Root-lesion nematodes ( <i>Pratylenchus thornei</i> )  |  | QTLs in 2BS, 6DS and 6DL  | CPI133872/Janz  | Zwart <i>et al.</i> (2010)   |
| <i>P. neglectus</i><br>Cereal cyst nematode ( <i>Heterodera avenae</i> )                                   | <i>Cre3</i>  | QTLs in 2BS and 6DS<br>QTLs in 2BS and 6DS<br>2DL                                       | ITMI population (W-7984/Opata 85)<br>CPI133872/Janz   | Zwart <i>et al.</i> (2006)<br>Zwart <i>et al.</i> (2010)<br>Eastwood <i>et al.</i> (1991)<br>Martin <i>et al.</i> (2004)           |
| Insects  |  |   |   |  |
| Hessian fly ( <i>Mayetiola destructor</i> )  | <i>H32</i><br><i>H26, H13</i>  | 3D  | Synthetic W-7984 (Altar 84/ <i>Ae. tauschii</i> )<br>SW8, SW34  | Sardesai <i>et al.</i> (2005)<br>Wang <i>et al.</i> (2006)   |
| Greenbug ( <i>Schizaphis graminum</i> )  | <i>Gb3</i> and <i>Gb7</i>  | 7DL   | Largo and W-7984  | Weng <i>et al.</i> (2005)  |

<sup>1</sup>, ITMI, International Triticeae Mapping Initiative population originating from a cross between the synthetic hexaploid wheat (*T. turgidum* cv. Altar 84 x *Ae. tauschii*) designated W7984 and the hard red spring wheat cv. Opata (M85);

<sup>2</sup>, *Snn1* is a host gene conferring sensitivity to SnTox1, a toxin that was partially purified from an isolate Sn2000 of *Stagonospora nodorum*.

blotch (STB) have been identified (Chartrain *et al.*, 2004), two of which, *Stb5* and *Stb8*, located on chromosomes 7DS and 7BL, respectively were recorded in SHWs (Table 3). *Stb8* is a single major gene controlling the resistance to STB in a population consisting of 130 recombinant-inbred lines derived from a cross between the SHW W7984 and cv. Opata 85 (Adhikari *et al.*, 2003).

Fusarium head blight (FHB) resistance in wheat is a quantitative trait controlled by several major and minor QTLs (Pumphrey *et al.*, 2007; Kang *et al.*, 2011) that were found on all wheat chromosomes except chromosome 7D. Some QTL were detected in several independent mapping studies indicating that such genes are stable and therefore useful in genetic and breeding tasks (Buerstmayr *et al.*, 2009). FHB resistance is not associated with *Ae. tauschii* but with the tetraploid parent. Hartel *et al.* (2004) found that FHB resistance carried by the 3A chromosome in *T. turgidum* ssp. *dicoccoides* was expressed in the resultant SHW. Eight near-isogenic lines were developed by marker-assisted backcrossing and, among them, lines that combined loci from 3BS and 2DL expressed the highest resistance and lowest deoxynivalenol content in four environments (Kang *et al.*, 2011).

Resistance of wheat to tan spot caused by *P. tritici-repentis* was reported to be quantitatively and qualitatively inherited, and that it was recessive and complex, involving at least four genes, which had not been located on D genome chromosomes in hexaploid wheat (Xu *et al.*, 2004). Instead, most of the tan spot resistance genes reported to date are located on the B genome of hexaploid wheat. The chromosomal location of the resistance genes identified in synthetics XX41, XX45 and XX110 was found on chromosome 3D. QTLs were detected in the genomes of all SHWs, confirming the polygenic control of this disease in wheat (Zwart *et al.*, 2010).

Resistance to insects has generally been associated with the D genome. Six (*H13*, *H22*, *H23*, *H24*, *H26* and *H32*) out of the 32 resistance genes identified originate from *Ae. tauschii* (Sardesai *et al.*, 2005). Three of them, *H13*, *H26* and *H32*, were reported in SHWs (Table 3). Two primary synthetics resistant to Hessian fly were registered for breeding practices (Xu *et al.*, 2006). Two dominant genes for resistance to greenbug (*Gb3* and *Gb7*) were reported in cvs Largo and W-7984 synthetic wheat (Weng *et al.*, 2005). In some lines epistatic interactions caused higher levels of resistance than either parent (Trethowan and van Ginkel, 2009).

In studies with CPI133872/Janz and the ITMI populations, chromosomes 2B and 6D were consistently found to bear QTLs for resistance to the nematodes *P. thornei* and *P. neglectus*. Additional minor genes were also found. The resistance appears to be polygenic, additive and greater when resistance genes from all three genomes (A, B and D) are present in the SHWs (Thompson *et al.*, 2008).

One gene (*Cre3*), located on chromosome 2DL, provides high levels of resistance to *Heterodera avenae* Woll. Martin *et al.* (2004) constructed genetic linkage maps of this wheat chromosome and identified microsatellite markers mapping close to the gene that enabled its use in marker-assisted selection and application in wheat breeding.

Genetic analysis for the resistance to biotic stresses is much complicated by many factors such as environmental effects and the presence of more than one resistance gene in a single line. Although the uniqueness of major genes and QTLs providing resistance in SHWs has in many cases yet to be established, significant variation is clearly present and emphasizes the importance of synthetic wheat gene pool for exploitation in breeding.

#### DEVELOPMENT OF SYNTHETIC-DERIVED BACKCROSSED WHEAT LINES AND CULTIVARS

The primary synthetics have been crossed to adapted wheats to obtain BC generations after 1-3 backcrosses following by self-pollinations (Valkoun, 2001; Dreccer *et al.*, 2007). Novel genotypes resulted from either new D- (from the diploid progenitor) or AB- (from tetraploid wheat) derived alleles or interactions between them and the bread wheat genome. Agronomically improved materials and/or synthetic-derived backcrossed (SDB) wheat lines, have been developed, showing superior yield performance compared to check cultivars (Dreisgacker *et al.*, 2008). The better adapted derivatives were generally those with a smaller portion (25% or less) of the primary synthetics in their pedigree. Dreccer *et al.* (2007) evaluated a different set of 156 derivatives developed by CIMMYT across the Australian wheat belt and found that 56% of the materials were higher yielding than the best local wheat cultivars. They indicated strong genotype x environment interactions and concluded that these differences in adaptation were likely caused by the length of the respective growing seasons and associated genotype specificity. Gororo *et al.* (2002) tested also SDB lines in Australia and Mexico, confirming their yield potential and fungal resistance across environments in both countries. Several high-yielding semi-dwarf wheat lines with good resistance to leaf blotch have been selected involving re-synthesized wheat lines as donors in their pedigree (Arraiano *et al.*, 2001; Ortiz *et al.*, 2008).

Lage and Trethowan (2008) evaluated the progeny derived from two backcrosses of adapted hexaploid wheat to a primary *T. turgidum* ssp. *dicoccon*-based synthetic hexaploid. They found some SDB lines showing significantly higher yield than the controls under stress conditions. Recently, to identify introgressed regions in synthetic derived lines, SSR markers spread across the wheat genome were used to locate a number of genes

inherited from both donors of D and AB genomes and their combinations in a selected genotype (Kunert *et al.*, 2007; Ibrahim *et al.*, 2010).

In 2003, Chuanmai 42, a cultivar obtained from one cross between a CIMMYT synthetic wheat and a local wheat variety, was released in China, producing 22.7% higher yields than the commercial control cv. Chuanmai 107 (Yang *et al.*, 2009). The new productive variety yielded large kernels and expressed resistance to stripe rust. Moreover, cv. Carmona, a synthetic wheat derivative that yields better grain quality has recently been released in Spain (Ortiz *et al.*, 2008).

## CONCLUDING REMARKS

Synthetic hexaploid wheats are useful sources of genetic improvement as they contain three genomes (A, B and D) deriving from tetraploid and diploid progenitors and, therefore, have the potential to recombine directly with their respective bread wheat genomes. These hexaploids provide new variability for resistance to fungi, nematodes and insects. Their promising traits are also connected with valuable morphological characteristics (large grain size, thousand kernel weight, plant height) and exhibit polymorphism for some seed quality properties, although these features were not addressed in the review.

Most of the primary synthetics derive from crosses with durum cultivars, and to a lesser extent with *T. turgidum* ssp. *dicoccon* and *dicoccoides*. New synthetic hexaploid wheats need to be synthesized and evaluated as sources of biotic stress resistance for exploiting more thoroughly the extant variation among other tetraploid wheats, with preference to ssp. *carthlicum*, *turanicum*, *paleocolchicum* and *polonicum*.

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