Broadening the Genetic Diversity of Bread Wheat Using Alien Germplasm: Emphasis on Disease Resistance

Vladimir Shumny, Elena Khlestkina, Irina Leonova and Elena Salina

Introduction

Broadening the genetic diversity for economically important traits is one of the main tasks of wheat genetics and breeding. There are many evidences of low allelic variability or loss of alleles related with yield, grain quality, and resistance to biotic and abiotic stresses among modern bread wheat varieties (Fu and Somers 2009; Gultyaeva 2012; Novoselskaya-Dragovich et al. 2015). The reduction in genetic diversity was accelerated in the second half of the 20th century, when a replacement of local wheat germplasm on high-yielding commercial cultivars took place. This has been demonstrated by analysis of pedigrees, phenotypic and molecular genetic assessments of plant material (Dreisigacker et al. 2004; Khlestkina et al. 2004).

Fungal diseases are among the major constraints that affect plant growth and yield of bread wheat (*Triticum aestivum* L.). Many efforts are focused on transfer of disease resistance genes from various cereal species of Triticeae tribe to the bread wheat genome.

T. aestivum belongs to one of the four *Triticum* genus sections—the *Triticum* section consisting of hexaploid wheat species with genome BA^uD. Further section (*Dicoccoides*) is represented by tetraploid emmer wheats with genome BA^u, and includes tetraploid progenitor of bread wheat, which hybrized with *Aegilops tauschii* Coss (genome D), resulting in formation of allohexaploid wheat (BA^uD) about 10,000 years ago. Other *Triticum* sections are *Monococcum* (diploid einkorn wheat with genomes A^u and A^b) and *Timopheevi* (tetraploid and hexaploid wheat species with genomes GA^u and GA^uA^b, respectively) (Goncharov 2002). Both the B and the G genomes are related to the S genome present in *Ae. speltoides* (Kimber 1974).

V. Shumny (✉) · E. Khlestkina · I. Leonova · E. Salina
Institute of Cytology and Genetics SBRAS, Lavrentjeva Ave. 10,
Novosibirsk 630090, Russia
e-mail: shumny@bionet.nsc.ru

V.L. Korogodina et al. (eds.), *Genetics, Evolution and Radiation*,
DOI 10.1007/978-3-319-48838-7_9

High similarity between *Ae. tauschii* and *T. aestivum* D-genome and the close evolutionary relationship between the B, S and G genomes allows for the relatively straightforward transfer of genetic information from *Ae. tauschii*, *Ae. speltoides* and *T. timopheevii* to bread wheat. Further Triticeae species (from *Aegilops*, *Secale* and *Hordeum* genera) also represent an important genetic reservoir for improvement of bread wheat (Friebe et al. 1996; Schneider et al. 2008; Trubacheeva et al. 2008; Pershina et al. 2009; Molnar-Lang et al. 2014). A wide range of wheat-alien lines has been developed over the past decades (Friebe et al. 1996, 2001; Wheat Genetics Resource Center). Synthetic wheats or lines with translocations and chromosome substitutions are often used as intermediate forms for gene transfer to varieties. The development of effective and usable genetic markers has made the process of heterologous gene transfer within the Triticeae tribe more efficient (Marais et al. 2001; Adonina et al. 2012; Chen et al. 2013; Timonova et al. 2013).

A number of resistance genes to leaf, stem, and yellow rusts and powdery mildew has been transferred into the genome of common wheat from wild and cultivated wheat relatives. Successful examples include the transfer of the *Lr9* and *Lr19* genes from *Ae. umbellulata* and *Th. ponticum* species (McIntosh et al. 1995). Until recently these genes remained effective against a broad set of leaf rust races (*Puccinia triticina* Eriks.) worldwide.

However, only a small number of the resistance genes described to date are used in breeding for development of resistant wheat varieties. Mainly this is due to the negative effects of foreign genetic material on agronomic traits.

In addition to wide application of alien germplasm for improvement of bread wheat resistance to fungal diseases, genes of various Triticeae species can be useful for increasing bread wheat tolerance to unfavorable environment conditions (reviewed in Colmer et al. 2006; Nevo and Chen 2010; Inbart-Pompan et al. 2013; recent examples are given in Yudina et al. 2015a, b), improvement of bread making quality (*Aegilops* ssp. genes: Kunert et al. 2007; Rehman et al. 2008; Garg et al. 2009; Sin et al. 2011; Wang et al. 2012, 2013; Zhou et al. 2014; *T. dicoccoides* Kunert et al. 2007) and nutrition properties: various *Triticum* ssp. and *Aegilops* ssp. genes can be used for increased production of iron and zink (Rawat et al. 2009) or antioxidant compounds (Khlestkina et al. 2010; Tereshchenko et al. 2012a, b).

Triticum Species for Bread Wheat Improvement

Hexaploid Wheats T. Spelta *and* T. Macha *(BA^{u}D)*

Hexaploid wheat *T. spelta* contributed to bread wheat resistance against septoria tritici blotch via substitution of chromosomes 2D, 5A, 5D, 6B, 6D and 7D (Simon et al. 2005). Two regions of chromosome 7D from spelt wheat were associated with isolate-specific resistance expressed at the seedling (locus *QStb.ipk-7D1)* and another at the adult (*QStb.ipk-7D2*) plant stage (Simon et al. 2010). The locus *QStb.ipk-7D2* was found on the short arm of chromosome 7D in a similar position to the locus *Lr34/Yr18* known to provide durable resistance against multiple pathogen races (Spielmeyer et al. 2008). Substituted chromosome 6B of hexaploid wheat *T. macha* is a carrier of a major determinant of head blight resistance, chromosomes 2A, 2B, 3A, 4A, 5A and 5B have also positive effect on resistance to these pathogens (Grausgruber et al. 1998; Steed et al. 2005; Buerstmayr et al. 2011; Burt et al. 2015).

Tetraploid Wheats T. Dicoccoides and T. Durum (BA^u)

Powdery mildew resistance genes were transferred from *T. dicoccoides* to bread wheat chromosomes 6AL (Xie et al. 2003) and 5BL (*PmAS846*; Xue et al. 2012). Other genes conferring resistance to this disease were found in *T. dicoccoides* chromosomes 5BL (*Pm36*; Blanco et al. 2008), 3BL (Li et al. 2009), 2BL (Maxwell et al. 2010) and 2BS (Hua et al. 2009; Liu et al. 2012).

T. dicoccoides leaf rust (*Lr53*) and stripe rust (*Yr35*) resistance genes were transferred to bread wheat chromosome 6BS (Marais et al. 2005). Other genes for stripe rust resistance were found in *T. dicoccoides* (*YrH52* and *Yr15*, Peng et al. 2000; *Yr36*, Uauy et al. 2005).

This species is also a potential donor of Fusarium head blight resistance genes (Hartel et al. 2004; Buerstmayr et al. 2013).

T. durum is a perspective donor of stem rust resistance gene *Sr13* (Simons et al. 2011). The role of *Sr13* and the role of chromosome regions putatively harboring *Sr9*, *Sr14*, *Sr17* and *Sr28* was shown for resistance to highly virulent stem rust race Ug99 (Letta et al. 2013).

T. durum resistance genes are often transferred to bread wheat via synthetic hexaploid forms obtained by crossing *T. durum* with *Ae. tauschii*. Genome-wide association study of 181 synthetic hexaploid wheats revealed a number of stripe rust resistance loci, including that on chromosomes of the A and B genomes of *T. durum*: 1AS, 1BS, 2AS, 2BL, 3BL, 5A, 5BL, and 7AL (Zegeye et al. 2014).

Molecular analysis of hybrid lines derived from crossing of Belarusian wheat varieties with *T. durum* suggested contribution of chromosomes 4B and 5B in the formation of the complex resistance to leaf rust, powdery mildew and septoriosis (Leonova et al. 2013).

Tetraploid Wheat **T. Timopheevii** *(GA^u)*

T. timopheevii was a donor of two stem rust resistance gene: *Sr36* and *Sr37* (McIntosh et al. 2013). The gene *Sr36* (formerly *SrTt1*) was used in breeding programs for more than 40 years. *Sr36* refers to a group of the genes, providing effective resistance to the most aggressive race of stem rust, Ug99 (Yu et al. 2014). For *Sr36* gene protocols for polymerase chain reaction were developed and diagnostic markers were designed for application in marker-assisted selection (MAS) programs.

The gene *Sr37* (*SrTt2*) despite its effectiveness against Ug99 was not used in breeding to improve the resistance of wheat varieties because of the significant negative effects of T4BL-4GL translocation on the productivity traits (McIntosh et al. 1995).

Two genes determining resistance to powdery mildew, *Pm6* and *Pm27*, were transferred from *T. timopheevii* ssp. *timopheevii* into chromosomes 2B and 6B respectively (Jørgensen and Jensen 1973; Järve et al. 2000). The gene *Pm6* was widely used for creation of resistant wheat varieties and is still one of the most effective genes in many regions of the world, including Europe, China and North America (Alam et al. 2011).

Three resistance genes with different efficiency to leaf rust (*Lr18*, *LrTt1*, and *LrTt2*), and two quantitative trait loci (*QLr.icg-1A, QLr.icg-2B*) were described in the genome of different subspecies of *T. timopheevii* (Yamamori 1994; Leonova et al. 2007, 2011). The gene *Lr18*, originating from *T. timopheevii* ssp. *timopheevii* has lost its efficacy against leaf rust races worldwide and is not currently used in breeding. The presence of the genes *LrTt1* and *LrTt2* (*T. timopheevii* var. *viticulosum*) and locus *QLr.icg-2B* (unknown subspecies of *T. timopheevii*) in wheat genotypes provides resistance to the wide range of leaf rust races in West Siberian regions of Russia (Leonova et al. 2007; Timonova et al. 2013). These loci have been used for creation of breeding lines and wheat cultivar “Pamyati Maistrenko” (Laikova et al. 2013).

Additionally, three genes determining resistance to leaf rust (*Lr50*), stem rust (*Sr40*) and powdery mildew (*Pm37*) were identified in the genome of wild subspecies *T. timopheevii* ssp. *armeniacum* (Brown-Guedira et al. 2003; Perugini et al. 2008; Wu et al. 2009).

Besides the aforementioned genes, there were evidences that wheat breeding lines with translocations from *T. timopheevii* contain genetic loci responsible for resistance to spot blotch, fusarium and septoriosis (Ma and Hughes 1995; Christopher et al. 2007; Srinivasachary et al. 2008).

Diploid Wheats T. Monococcum (A^m) and T. Boeoticum (A^b)

Stem rust resistance genes *Sr21*, *Sr22*, and *Sr35* were transferred from diploid wheat *T. monococcum* to bread wheat (Kerber and Dyck 1973; Rouse and Jin 2011). *Sr21* (Chen et al. 2015) and a number of other *T. monococcum* stem rust resistance genes different from *Sr21*, *Sr22*, and *Sr35* (2 genes, Rouse and Jin 2011; gene *SrTm4*, Briggs et al. 2015) confer resistance to highly virulent stem rust race Ug99.

Two powdery mildew resistance genes (*PmTb7A.1* and *PmTb7A.2*) were identified and mapped on chromosome 7AL of another diploid wheat species, *T. boeoticum* (Chhuneja et al. 2012, 2015).

Aegilops Species for Wheat Improvement

Ae. Speltoides

Ae. speltoides, which is characterized by a high grain protein content along with fungal diseases resistance, was a donor of the leaf rust resistance genes *Lr28, Lr35, Lr36, Lr47*, and *Lr51* (reviewed in Schneider et al. 2008; Todorovska et al. 2009). Among recent examples, genes encoding leaf rust resistance have been transferred from *Ae. speltoides* into *T. aestivum* (Adonina et al. 2012). *Lr28*, *Lr36* and *Lr47* genes were shown to be highly effective against leaf rust populations in most regions of the world, although, with the exception of the *Lr28*, remaining genes were not widely used in breeding practice for development of resistant wheat cultivars due to negative effects on agronomic traits.

Ae. speltoides is also a source of *Sr32, Sr39*, *Sr47*, and *SrAes7t* genes providing resistance of common and durum wheats to stem rust including race Ug99 (McIntosh et al. 1995; Faris et al. 2008; Klindworth et al. 2012; Yu et al. 2014).

Two *Ae. speltoides* powdery mildew resistance genes (*Pm12* and *Pm32*) were introgressed into common wheat chromosomes 6BL and 1BL respectively (McIntosh et al. 1995; Hsam et al. 2003). *Pm12* is very effective against populations of powdery mildew pathogen worldwide. But this gene is not widely used in wheat breeding because of negative influence of alien chromatin on wheat productivity (Song et al. 2007).

Recently gene *Pm53* was located on the long arm of chromosome 5BL of winter wheat germplasm line and appears to be a new source of powdery mildew resistance that can be tracked with molecular markers in MAS schemes (Petersen et al. 2015).

Ae. Tauschii

Ae. tauschii, the D genome donor of bread wheat has been used extensively for the transfer of agronomic important traits to wheat, including leaf rust resistance genes *Lr41*, *Lr42*, and *Lr43* (Cox et al. 1994) as well as stem rust resistance genes *Sr33* (1DS), *Sr45* (1DS), and *Sr46* (2DS) conferring resistance to highly virulent race Ug99 (Rouse and Jin 2011; Yu et al. 2015). It was shown later that *Lr40* is the same gene as *Lr21*, while *Lr41* is a synonym of *Lr39*. *Lr43* is not a unique gene because initial germplasm lines consist of the progenies with gene combination (*Lr21* and *Lr39*) (McIntosh et al. 2013).

Other two Ug99-effective stem rust resistance genes were recently transferred to bread wheat from chromosomes 6DS (*SrTA10187*) and 7DS (*SrTA10171*) of *Ae. tauschii* (Olson et al. 2013).

Ae. tauschii is often used for introgression of resistance genes into the genome of bread wheat through the development of synthetic hexaploid forms. Association mapping with the help of a set of synthetic hexaploid wheats revealed 2 novel stripe rust resistance loci on chromosomes 3DL and 6DS originating from *Ae. tauschii* (Zegeye et al. 2014). Stripe rust resistance genes were revealed on *Ae. tauschii* chromosomes 3DS (*YrY206*, Zhang et al. 2009) and 4DS (*YrAS2388*, Huang et al. 2011). Potential of this species for improvement of stripe rust resistance was also shown by Liu et al. (2013).

Miranda et al. (2006, 2007) identified *Ae. tauschii*-derived wheat powdery mildew resistance genes *Pm34* and *Pm35* on wheat chromosome 5D. Sun et al. (2006) mapped 2 genes, *PmY201* and *PmY212*, on chromosome 5DL of *Ae. tauschii*. Maxwell et al. (2012) characterized a novel *Ae. tauschii*-derived gene (*MlNCD1*) conferring resistance to powdery mildew, mapped to the short arm of chromosome 7D in more distal position compared to the previously known *Pm38* gene.

Other Aegilops Species

Germplasm of the other *Aegilops* species (not related with hexaploid wheat origin) has been exploited to a limited extent for a search and transfer of the genes determining wheat resistance to fungal diseases. This is primarily due to methodological difficulties of introduction of foreign genetic material into the genome of common wheat by direct hybridization. Nevertheless, a number of genes for resistance to rust diseases was identified in the genomes of *Ae. ventricosa* (*Lr37, Yr17, Sr38*), *Ae. geniculata* (*Lr57*, *Yr40*, *Sr53*), *Ae. triuncialis* (*Lr58*), and *Ae. peregrina* (*Lr59*) (Seah et al. 2001; Kuraparthy et al. 2007a, b; Marais et al. 2008)

For translocation T5DL•5DS-5MgS from *Ae. geniculata*, containing leaf and stripe rust resistance genes (*Lr57, Yr40*) the absence of negative effects on endosperm texture of winter wheat cultivars has been proven (Kuraparthy et al. 2009). Positive effects on bread-making quality was detected for translocation containing cluster *Lr37-Yr17-Sr38* genes from *Ae. ventricosa* (Labuschagne et al. 2002).

A number of disease resistance genes have been transferred from other *Aegilops* species: *Ae. umbellulata* (*LrU1, LrU2, YrU1*), *Ae. caudata* (*LrAC*), *Ae. variabilis* (unknown gene), and *Ae. variabilis* (*LrV, YrV*) (Chhuneja et al. 2008; Riar Kaur et al. 2012; Spetsov et al. 2013). Apparent linkage drag was observed neither in the introgression lines obtained on the basis of *Ae. umbellulata* and *Ae. variabilis*, nor in their backcross progenies, suggesting that new genetic loci could be exploited commercially.

Rye as a Source of Disease Resistance Genes for Bread Wheat

Among the successful introduction of rye (*Secale cereale* L.) genetic material into the genome of common wheat only two translocations have practical value, and in both cases chromosome 1RS took part in these translocations.

The translocated 1RS chromosome arm of the rye cultivar 'Kavkaz' frequently occurs in wheat cultivars of European selection (Villareal et al. 1998; Purnhauser et al. 2011). It confers disease resistance against powdery mildew (*Pm8*), stem rust (*Sr31*), leaf rust (*Lr26*) and stripe rust (*Yr9*) (Lukaszewski 2000). Cultivars with this so-called 1BL.1RS translocation (Mettin et al. 1973; Zeller 1973) showed high yield potential and multiple disease resistance (Rabinovich 1998; Kim et al. 2004; Belan et al. 2010).

Translocation 1AL.1RS, obtained on the basis of rye cultivar 'Amigo' contains genes for resistance to wheat aphid (*Gb2*), powdery mildew (*Pm17*) and stem rust (unknown gene). This translocation is spread mainly in the American wheat varieties. Translocation 1AL.1RS was also found to have positive effects on drought tolerance, grain protein content and yield (McIntosh et al. 1995; Kim et al. 2004).

Other wheat-rye translocations, such as T3AS-3RS with *Sr27* gene, T4BS.4BL-5RL with *Lr25*, T6BS-6RL with *Pm20*, T2AS-2RS.2RL with *Lr45*, and T2BS-2RL containing the locus of resistance to Hessian fly are not widely used in breeding due to their negative effects on agronomic traits.

Conclusions and Prospects

Wild and cultivated wheat relatives and species from related genera are an inexhaustible source of genes providing resistance to diseases and insects. To date, more than 50 % of known genes determining resistance to rust diseases and powdery mildew originate from wheat relatives (McIntosh et al. 2013). However, only a limited number of genes were utilized in practical breeding to improve genetic basis of bread wheat resistance. Others were used only for development of introgression and isogenic lines.

One of the main reasons for limited practical application of the resistance genes is the presence of alien genetic material tightly linked with the target gene and negatively influencing agronomic traits. For example gene *Lr19* closely linked to the gene *Y*, determining the yellow color of flour is not used for development of resistance of wheat cultivars in those countries which traditionally prefer the flour of white color.

In recent years, the development of new molecular methods for tagging of disease resistance genes and technology of marker-assisted selection made it possible to eliminate excessive donor material, which may have negative effect on agronomic traits. In this way, for example, bread wheat lines with shorter introgression fragments containing *Sr37* and *Sr39* genes with effective resistance to stem rust were obtained (Yu et al. 2010; Zhang et al. 2012). The study demonstrated that the lines with reduced alien chromatin have no negative effects on productivity traits anymore.

Further difficulties can be related with insufficient level of alien gene expression due to divergence between bread wheat *cis*- or *trans*-regulatory elements and those of the donor species (Khlestkina et al. 2009; Shoeva et al. 2016) or suppression of alien genes by their orthologs in wheat (Hurni et al. 2014).

The recently developed approach for precise gene editing, CRISPR/Cas9 system (reviewed in Bortesi and Fischer 2015), has been already used successfully for editing resistance genes in wheat (Wang et al. 2014). This system allows making fine changes in plant genome and may help to overcome the difficulties mentioned above by editing regulatory sequences or direct insertion of desirable gene sequences without hybridization.

References

Adonina IG, Petrash NV, Timonova EM, Khristov YA, Salina EA (2012) Construction and study of leaf rust-resistant common wheat lines with translocations of *Aegilops speltoides* Tausch. genetic material. Russ J Genet 48:404–409

Alam MA, Xue F, Wang C, Ji W (2011) Powdery mildew resistance genes in wheat: identification and genetic analysis. J Mol Biol Res 1:20–39

Blanco A, Gadaleta A, Cenci A, Carluccio AV, Abdelbacki AM, Simeone R (2008) Molecular mapping of the novel powdery mildew resistance gene *Pm36* introgressed from *Triticum turgidum* var. *dicoccoides* in durum wheat. Theor Appl Genet 117:135–242

Belan IA, Rosseeva LP, Trubacheeva NV, Osadchaya TS, Dorogina OV, Zhmud EV, Kolmakov YV, Blokhina NP, Kravtsova LA, Pershina LA (2010) Some agronomic important features of spring wheat cultivar Omskaya 37 lines containing wheat-rye translocation 1RS.1BL. Vavilov J Genet Breed 14:632–640 (Russian)

Bortesi L, Fischer R (2015) The CRISPR/Cas9 system for plant genome editing and beyond. Biotechnol Adv 33:41–52

Brown-Guedira GL, Singh S, Fritz AK (2003) Performance and mapping of leaf rust resistance transferred to wheat from *Triticum timopheevii* subsp. *armeniacum*. Phytopathology 93:784–789

Briggs J, Chen S, Zhang W, Nelson S, Dubcovsky J, Rouse MN (2015) Mapping of *SrTm4*, a recessive stem rust resistance gene from diploid wheat effective to Ug99. Phytopathology 105:1347–1354

Buerstmayr M, Lemmens M, Steiner B, Buerstmayr H (2011) Advanced backcross QTL mapping of resistance to Fusarium head blight and plant morphological traits in a *Triticum macha* × *T. aestivum* population. Theor Appl Genet 123:293–306

Buerstmayr M, Alimari A, Steiner B, Buerstmayr H (2013) Genetic mapping of QTL for resistance to Fusarium head blight spread (type 2 resistance) in a *Triticum dicoccoides* × *Triticum durum* backcross-derived population. Theor Appl Genet 126:2825–2834

Burt C, Steed A, Gosman N, Lemmens M, Bird N, Ramirez-Gonzalez R, Holdgate S, Nicholson P (2015) Mapping a Type 1 FHB resistance on chromosome 4AS of *Triticum macha* and deployment in combination with two Type 2 resistances. Theor Appl Genet 128:1725–1738

Chen P, You C, Hu Y, Chen S, Zhou B, Cao A, Wang X (2013) Radiation-induced translocations with reduced *Haynaldia villosa* chromatin at the *Pm21* locus for powdery mildew resistance in wheat. Mol Breed 31:477–484

Chen S, Rouse MN, Zhang W, Jin Y, Akhunov E, Wei Y, Dubcovsky J (2015) Fine mapping and characterization of *Sr21*, a temperature-sensitive diploid wheat resistance gene effective against the *Puccinia graminis* f. sp. *tritici* Ug99 race group. Theor Appl Genet 128:645–656

Chhuneja P, Kaur S, Goel RK, Aghaee-Sarbarzeh M, Prashar M, Dhaliwal HS (2008) Transfer of leaf rust and stripe rust resistance from *Aegilops umbellulata* Zhuk. to bread wheat (*Triticum aestivum* L.). Genet Resour Crop Evol 55:849–859

Chhuneja P, Kumar K, Stirnweis D, Hurni S, Keller B, Dhaliwal HS, Singh K (2012) Identification and mapping of two powdery mildew resistance genes in *Triticum boeoticum* L. Theor Appl Genet 124:1051–1058

Chhuneja P, Yadav B, Stirnweis D, Hurni S, Kaur S, Elkot AF, Keller B, Wicker T, Sehgal S, Gill BS, Singh K (2015) Fine mapping of powdery mildew resistance genes *PmTb7A.1* and *PmTb7A.2* in *Triticum boeoticum* (Boiss.) using the shotgun sequence assembly of chromosome 7AL. Theor Appl Genet 128:2099–2111

Christopher MJ, Williamson PM, Michalowitz M, Jennings R, Lehmensiek A, Sheppard J, Banks P (2007) Simple sequence repeat markers associated with three quantitative trait loci for black point resistance can be used to enrich selection populations in bread wheat. Austr J Agricult Res 58:867–873

Colmer TD, Flowers TJ, Munns R (2006) Use of wild relatives to improve salt tolerance in wheat. J Exp Bot 57:1059–1078

Cox TS, Raupp WJ, Gill BS (1994) Leaf rust-resistance genes *Lr41*, *Lr42*, and *Lr43* transferred from *Triticum tauschii* to common wheat. Crop Sci 34:339–343

Dreisigacker S, Zhang P, Warburton ML, van Ginkel M, Hoisington D, Bohnband M, Melchinger AE (2004) SSR and pedigree analyses of genetic diversity among CIMMYT wheat lines targeted to different megaenvironments. Crop Sci 44:381–388

Faris JD, Xu SS, Cai X, Friesen TL, Jin Y (2008) Molecular and cytogenetic characterization of a durum wheat-*Aegilops speltoides* chromosome translocation conferring resistance to stem rust. Chromosome Res 16:1097–1105

Friebe B, Jiang J, Raupp WJ, McIntosh RA, Gill BS (1996) Characterization of wheat-alien translocations conferring resistance to diseases and pests: current status. Euphytica 91:59–87

Friebe B, Raupp WJ, Gill BS (2001) Alien genes in wheat improvement. In: Bedo Z, Lang L (eds) Wheat in a global environment. Kluver Academic Publisher, Dordrecht, pp 709–720

Fu YB, Somers DJ (2009) Genome wide reduction of genetic diversity in wheat breeding. Crop Sci 49:161–168

Garg M, Tanaka H, Ishikawa N, Takata K, Yanaka M, Tsujimoto H (2009) A novel pair of HMW glutenin subunits from *Aegilops searsii* improves quality of hexaploid wheat. Cereal Chem 86:26–32

Goncharov NP (2002) Comparative genetics of wheats and their related species. Siberian un-ty press, Novosibirsk (Russian)

Grausgruber H, Lemmens M, Bürstmayr H, Ruckenbauer P (1998) Chromosomal location of Fusarium head blight resistance and in vitro toxin tolerance in wheat using the Hobbit 'sib' (*Triticum macha*) chromosome substitution lines. J Genet Breed 52:173–180

Gultyaeva EI (2012) Genetic diversity of Russian wheat cultivars for resistance to leaf rust. Rep Russ Acad Agric Sci 2:29–32 (Russian)

Hartel KD, Berzonsky WA, Kianian SF, Ali S (2004) Expression of a *Triticum turgidum* var. *dicoccoides* source of Fusarium head blight resistance transferred to synthetic hexaploid wheat. Plant Breed 123:516–519

Hsam SLK, Lapochkina IF, Zeller FJ (2003) Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 8. Gene *Pm32* in a wheat *Aegilops speltoides* translocation line. Euphytica 133:367–370

Hua W, Liu Z, Zhu J, Xie C, Yang T, Zhou Y, Duan X, Sun Q, Liu Z (2009) Identification and genetic mapping of *pm42*, a new recessive wheat powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). Theor Appl Genet 119:223–230

Huang L, Zhang L-Q, Liu B-L, Yan Z-H, Zhang B, Zhang H-G, Zheng Y-L, Liu D-C (2011) Molecular tagging of a stripe rust resistance gene in *Aegilops tauschii*. Euphytica 179:313–318

Hurni S, Brunner S, Stirnweis D, Herren G, Peditto D, McIntosh RA, Keller B (2014) The powdery mildew resistance gene *Pm8* derived from rye is suppressed by its wheat ortholog *Pm3*. Plant J 79:904–913

Inbart-Pompan H, Eilam T, Eshe A (2013) Searching for salt tolerance among wild relatives of wheat: what should we look for? Aust J Crop Sci 7:2116–2127

Järve K, Peusha HO, Tsymbalova J, Tamm S, Devos KM, Enno TM (2000) Chromosomal location of *Triticum timopheevii* derived powdery mildew resistance genes transferred to common wheat. Genome 43:377–381

Jørgensen JH, Jensen CJ (1973) Gene *Pm6* for resistance to powdery mildew in wheat. Euphytica 22:4–23

Kerber ER, Dyck PL (1973) Inheritance of stem rust resistance transferred from diploid wheat (*Triticum monococcum*) to tetraploid and hexaploid wheat and chromosome location of the gene involved. Canadian J Genet Cytol 15:397–409

Khlestkina EK, Salina EA, Shumny VK (2004) Genotyping of native varieties of soft wheat by the microsatellite (SSR) markers. Sel'skokhozyaistvennaya Biologiya [Agric Biol] 5:44–52 (Russian)

Khlestkina EK, Tereshchenko OY, Salina EA (2009) Anthocyanin biosynthesis genes location and expression in wheat-rye hybrids. Mol Genet Genomics 282:475–485

Khlestkina EK, Röder MS, Börner A (2010) Mapping genes controlling anthocyanin pigmentation on the glume and pericarp in tetraploid wheat (*Triticum durum* L.). Euphytica 171:65–69

Kim W, Jonson PS, Baenziger PS, Lukaszewski AJ, Gaines CS (2004) Agronomic effect of wheat-rye translocation carrying rye chromatin (1R) from different sources. Crop Sci 44:1254–1258

Kimber G (1974) A reassessment of the origin of the polyploid wheats. Genetics 78:487–492

Klindworth DL, Niu Z, Chao S, Friesen TL, Jin Y, Faris JD, Cai X, Xu SS (2012) Introgression and characterization of a Goatgrass gene for a high level of resistance to Ug99 stem rust in tetraploid wheat. G3-Genes Genomes Genet 2:665–673

Kunert A, Naz AA, Dedeck O, Pillen K, Léon J (2007) AB-QTL analysis in winter wheat: I. Synthetic hexaploid wheat (*T. turgidum* ssp. *dicoccoides* x *T. tauschii*) as a source of favorable alleles for milling and baking quality traits. Theor Appl Genet 115:683–695

Kuraparthy V, Chhuneja P, Dhaliwal HS, Kaur S, Bowden RL, Gill BS (2007a) Characterization and mapping of cryptic alien introgression from *Aegilops geniculata* with new leaf rust and stripe rust resistance genes *Lr57* and *Yr40* in wheat. Theor Appl Genet 114:1379–1389

Kuraparthy V, Sood S, Chhuneja P, Dhaliwal HS, Kaur S, Bowden RL, Gill BS (2007b) A cryptic wheat–*Aegilops triuncialis* translocation with leaf rust resistance gene *Lr58*. Crop Sci 47:1995–2003

Kuraparthy V, Sood S, See DR, Gill BS (2009) Development of a PCR assay and marker-assisted transfer of leaf rust and stripe rust resistance genes *Lr57* and *Yr40* into hard red winter wheats. Crop Sci 49:120–126

Labuschagne MT, Pretorius ZA, Grobbelaar B (2002) The influence of leaf rust resistance genes *Lr29, Lr34, Lr35* and *Lr37* on bread making quality in wheat. Euphytica 124:65–70

Laikova LI, Belan IA, Badaeva ED, Rosseeva LP, Shepelev SS, Shumny VK, Pershina LA (2013) Development and study of spring bread wheat variety Pamyati Maystrenko with introgression of genetic material from synthetic hexaploid *Triticum timopheevii* Zhuk. × *Aegilops tauschii* Coss. Rus J Genet 49:89–97

Leonova IN, Laikova LI, Popova OM, Unger O, Börner A, Röder MS (2007) Detection of quantitative trait loci for leaf rust resistance in wheat—*T. timopheevii/T. tauschii* introgression lines. Euphytica 155:79–86

Leonova IN, Budashkina EB, Kalinina NP, Röder MS, Börner A, Salina EA (2011) *Triticum aestivum*—*Triticum timopheevii* introgression lines as a source of pathogen resistance genes. Czech J Genet Plant Breed 47:S49–S55

Leonova IN, Badaeva ED, Orlovskaya OA, Röder MS, Khotyleva LV, Salina EA, Shumny VK (2013) Comparative characteristic of *Triticum aestivum/Triticum durum* and *Triticum aestivum/Triticum dicoccum* hybrid lines by genomic composition and resistance to fungal diseases under different environmental conditions. Rus J Genet 49:1112–1118

Letta T, Maccaferri M, Badebo A, Ammar K, Ricci A, Crossa J, Tuberosa R (2013) Searching for novel sources of field resistance to Ug99 and Ethiopian stem rust races in durum wheat via association mapping. Theor Appl Genet 126:1237–1256

Li G, Fang T, Zhang H, Xie C, Li H, Yang T, Nevo E, Fahima T, Sun Q, Liu Z (2009) Molecular identification of a new powdery mildew resistance gene *Pm41* on chromosome 3BL derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). Theor Appl Genet 119:531–539

Liu Z, Zhu J, Cui Y, Liang Y, Wu H, Song W, Liu Q, Yang T, Sun Q, Liu Z (2012) Identification and comparative mapping of a powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*) on chromosome 2BS. Theor Appl Genet 124:1041–1049

Liu M, Zhang C, Yuan C, Zhang L, Huang L, Wu J, Wang J, Zheng Y, Zhang H, Liu D, Fu D (2013) Stripe rust resistance in *Aegilops tauschii* germplasm. Crop Sci 53:2014–2020

Lukaszewski AJ (2000) Manipulation of the 1RS.1BL translocation in wheat by induced homoeologous recombination. Crop Sci 40:216–225

Ma H, Hughes GR (1995) Genetic control and chromosomal location of *Triticum timopheevii*-derived resistance to septoria nodorum blotch in durum wheat. Genome 38:332–338

Marais GF, Marais AS, Groenewald JZ (2001) Evaluation and reduction of *Lr19*-149, a recombined form of the *Lr19* translocation of wheat. Euphytica 121:289–295

Marais GF, Pretorius ZA, Wellings CR, McCallum B, Marais AS (2005) Leaf rust and stripe rust resistance genes transferred to common wheat from *Triticum dicoccoides*. Euphytica 143:115–123

Marais GF, McCallum B, Marais AS (2008) Wheat leaf resistance gene *Lr59* derived from *Aegilops peregrina*. Plant Breed 127:340–345

Maxwell JJ, Lyerly JH, Srnic G, Parks R, Cowger C, Marshall D, Brown-Guedira G, Murphy JP (2010) *MlAB10*: A *Triticum turgidum* subsp. *dicoccoides* derived powdery mildew resistance gene identified in common wheat. Crop Sci 50:2261–2267

Maxwell JJ, Lyerly JH, Srnic G, Murphy JP, Cowger C, Parks R, Marshall D, Brown-Guedira G, Miranda L (2012) *MlNCD1*: A novel *Aegilops tauschii*—derived powdery mildew resistance gene identified in common wheat. Crop Sci 52:1162–1170

McIntosh RA, Wellings CR, Park RF (1995) Wheat rust: an atlas of resistance genes. CSIRO Publishing, Australia, p 200

McIntosh RA, Yamazaki Y, Dubcovsky J, Rogers J, Morris C, Appels R, Xia XC (2013) Catalogue of gene symbols for wheat. Available at: http://www.shigen.nig.ac.jp/wheat/komugi/genes/

Mettin D, Bluthner WD, Schlegel G (1973) Additional evidence on spontaneous 1B/1R wheat-rye substitutions and translocations. In: Sears ER, Sears LMS (eds) Proceedings of the 4th international wheat genetics symposium. University of Missouri, Columbia, pp 179–184

Miranda LM, Murphy JP, Marshall D, Leath S (2006) *Pm34*: A new powdery mildew resistance gene transferred from *Aegilops tauschii* Coss. to common wheat (*Triticum aestivum* L.). Theor Appl Genet 113:1497–1504

Miranda LM, Murphy JP, Marshall D, Cowger C, Leath S (2007) Chromosomal location of *Pm35*, a novel *Aegilops tauschii* derived powdery mildew resistance gene introgressed into common wheat (*Triticum aestivum* L.). Theor Appl Genet 114:1451–1456

Molnar-Lang M, Line G, Szakacs E (2014) Wheat–barley hybridization: the last 40 years. Euphytica 195:315–329

Nevo E, Chen G (2010) Drought and salt tolerances in wild relatives for wheat and barley improvement. Plant Cell Environ 33:670–685

Novoselskaya-Dragovich AY, Bespalova LA, Shishkina AA, Melnik VA, Upelniek VP, Fisenko AV, Dedova LV, Kudryavtsev AM (2015) Genetic diversity of common wheat varieties at the gliadin-coding loci. Rus J Genet 51:262–271

Olson EL, Rouse MN, Pumphrey MO, Bowden RL, Gill BS, Poland JA (2013) Introgression of stem rust resistance genes *SrTA10187* and *SrTA10171* from *Aegilops tauschii* to wheat. Theor Appl Genet 126:2477–2484

Peng JH, Fahima T, Röder MS, Huang QY, Dahan A, Li YC, Grama A, Nevo E (2000) High-density molecular map of chromosome region harboring stripe-rust resistance genes *YrH52* and *Yr15* derived from wild emmer wheat, *Triticum dicoccoides*. Genetica 109:199–210

Pershina LA, Devyatkina EP, Belova LI, Trubacheeva NV, Arbuzova VS, Kravtsova LA (2009) Features of alloplasmic wheat-barley substitution and addition lines (*Hordeum marinum* subsp. *gussoneanum*)-*Triticum aestivum*. Russ J Genet 45:1223–1229

Perugini LD, Murphy JP, Marshall DS, Brown-Guedira G (2008) *Pm37*, a new broadly effective powdery mildew resistance gene from *Triticum timopheevii*. Theor Appl Genet 116:417–425

Petersen S, Lyerly JH, Worthington ML, Parks WR, Cowger C, Marshall DS, Brown-Guedira G, Murphy JP (2015) Mapping of powdery mildew resistance gene *Pm53* introgressed from *Aegilops speltoides* into soft red winter wheat. Theor Appl Genet 128:303–312

Purnhauser L, Bona L, Lang L (2011) Occurrence of 1BL.1RS wheat-rye chromosome translocation and of *Sr36/Pm6* resistance gene cluster in wheat cultivars registered in Hungary. Euphytica 179:287–295

Rabinovich SV (1998) Importance of wheat-rye translocations for breeding modern cultivars of *Triticum aestivum* L. Euphytica 100:323–340

Rawat N, Tiwari VK, Singh N, Randhawa GS, Singh K, Chhuneja P, Dhaliwal HS (2009) Evaluation and utilization of Aegilops and wild Triticum species for enhancing iron and zinc content in wheat. Gen Res Crop Evol 56:53–64

Rehman A, Evans N, Gianibelli MC, Rose RJ (2008) Allelic variations in high and low molecular weight glutenins at the *Glu-Dt* locus of *Aegilops tauschii* as a potential source for improving bread wheat quality. Aust J Agricult Res 59:399–405

Riar Kaur A, Kaur S, Dhaliwal YS, Singh K, Chhuneja P (2012) Introgression of a leaf rust resistance gene from *Aegilops caudata* to bread wheat. J Genet 91:155–161

Rouse MN, Jin Y (2011) Genetics of resistance to race TTKSK of *Puccinia graminis* f. sp. *tritici* in *Triticum monococcum*. Phytopathology 101:1418–1423

Schneider A, Molnár I, Molnár-Láng M (2008) Utilization of Aegilops (goatgrass) species to widen of genetic diversity of cultivated wheat. Euphytica 163:1–19

Seah S, Bariana H, Jahier J, Sivasithamparum K, Lagudah ES (2001) The introgressed segment carrying rust resistance genes *Yr17, Lr37* and *Sr38* in wheat can be assayed by a cloned disease resistance gene-like sequence. Theor Appl Genet 102:600–605

Shoeva OY, Dobrovolskaya OB, Leonova IN, Salina EA, Khlestkina EK (2016) The B-, G- and S-genomic *Chi* genes in Triticeae. Biologia Plant 60:279–284

Simon MR, Worland CA, Struik PC (2005) Chromosomal location of genes encoding for resistance to septoria tritici blotch (*Mycosphaerella graminicola*) in substitution lines of wheat. Neth J Agric Sci 53:113–129

Simon MR, Khlestkina EK, Castillo NS, Börner A (2010) Mapping quantitative resistance to septoria tritici blotch in spelt wheat. Eur J Plant Pathol 128:317–324

Simons K, Abate Z, Chao S, Zhang W, Rouse M, Jin Y, Elias E, Dubcovsky J (2011) Genetic mapping of stem rust resistance gene *Sr13* in tetraploid wheat (*Triticum turgidum* ssp. *durum* L.). Theor Appl Genet 122:649–658

Sin E, del Moral J, Hernández P, Benavente E, Rubio M, Martín-Sánchez JA, Pérez RF, López-Braña I, Delibes A (2011) Effects of the 4N(v) chromosome from *Aegilops ventricosa* on agronomic and quality traits in bread wheat. Czech J Genet Plant Breed 47:S63–S66

Song W, Xice H, Liu Q, Xice CJ, Ni ZF, Jang TM, Sun QX, Liu ZY (2007) Molecular identification of *Pm12*—carrying introgression lines in wheat using genomic and EST-SSR markers. Euphytica 158:95–102

Spetsov P, Daskalova N, Plamenov D, Moraliyski T (2013) Resistance to powdery mildew and leaf rust in wheat lines derived from a *Triticum aestivum/Aegilops variabilis* cross. Turkish J Field Crops 18:128–133

Spielmeyer W, Singh RP, McFadden H, Wellings CR, Huerta-Espino J, Kong X, Appels R, Lagudah ES (2008) Fine scale genetic and physical mapping using interstitial deletion mutants of *Lr34/Yr18*: a disease resistance locus effective against multiple pathogens in wheat. Theor Appl Genet 116:481–490

Srinivasachary Gosman N, Steed A, Faure S, Bayles R, Jennings P, Nicholson P (2008) Mapping of QTL associated with Fusarium head blight in spring wheat RL4137. Czech J Genet Plant Breed 44:147–159

Steed A, Chandler E, Thomsett M, Gosman N, Faure S, Nicholson P (2005) Identification of type I resistance to Fusarium head blight controlled by a major gene located on chromosome 4A of *Triticum macha*. Theor Appl Genet 111:521–529

Sun X-L, Liu D, Zhang H-Q, Huo N-X, Zhou R-Z, Jia J-Z (2006) Identification and mapping of two new genes conferring resistance to powdery mildew from *Aegilops tauschii* (Coss.) schmal. J Integr Plant Biol 48:1204–1209

Tereshchenko OY, Pshenichnikova TA, Salina EA, Khlestkina EK (2012a) Development and molecular characterization of a novel wheat genotype having purple grain colour. Cereal Res Commun 40:210–214

Tereshchenko OY, Gordeeva EI, Arbuzova VS, Börner A, Khlestkina EK (2012b) The D genome carries a gene determining purple grain colour in wheat. Cereal Res Commun 40:334–341

Timonova EM, Leonova IN, Röder MS, Salina E (2013) Marker-assisted development and characterization of a set of *Triticum aestivum* lines carrying different introgressions from the *T. timopheevii* genome. Mol Breed 31:123–136

Todorovska E, Christov N, Slavov S, Christova P, Vassilev D (2009) Biotic stress resistance in wheat—breeding and genomic selection implications. Biotechnol Biotec Eq 23:1417–1426

Trubacheeva NV, Badaeva ED, Adonina IG, Belova LI, Devyatkina EP, Pershina LA (2008) Construction and molecular and cytogenetic analyses of euploid ($2n$ = 42) and telocentric addition ($2n$ = 42 + 2t) alloplasmic lines (*Hordeum marinum* subsp. *gussoneanum*)-*Triticum aestivum*. Russ J Genet 44:67–73

Uauy C, Brevis JC, Chen X, Khan I, Jackson L, Chicaiza O, Distelfeld A, Fahima T, Dubcovsky J (2005) High-temperature adult-plant (HTAP) stripe rust resistance gene *Yr36* from *Triticum turgidum* ssp. *dicoccoides* is closely linked to the grain protein content locus *Gpc-B1*. Theor Appl Genet 112:97–105

Villareal RL, Banuelos O, Mujeeb-Kazi A, Rajaram S (1998) Agronomic performance of chromosome 1B and T1BL.1RS near-isolines in the spring bread wheat Seri M82. Euphytica 103:195–202

Wang K, An XL, Pan LP, Dong K, Gao LY, Wang SL, Xie ZZ, Zhang Z, Appels R, Ma W, Yan YM (2012) Molecular characterization of HMW-GS 1Dx3(t) and 1Dx4(t) genes from *Aegilops tauschii* and their potential value for wheat quality improvement. Hereditas 149:41–49

Wang S, Yu Z, Cao M, Shen X, Li N, Li X, Ma W, Weißgerber H, Zeller F, Hsam S, Yan Y (2013) Molecular mechanisms of HMW glutenin subunits from 1S(l) genome of *Aegilops longissima* positively affecting wheat breadmaking quality. PLoS ONE 8:e58947

Wang Y, Cheng X, Shan Q, Zhang Y, Liu J, Gao C, Qiu JL (2014) Simultaneous editing of three homoeoalleles in hexaploid breadwheat confers heritable resistance to powdery mildew. Nat Biotechnol 32:947–951

Wu SG, Pumphrey M, Bai GH (2009) Molecular mapping of stem-rust-resistance gene *Sr40* in wheat. Crop Sci 49:1681–1686

Xie C, Sun Q, Ni Z, Yang T, Nevo E, Fahima T (2003) Chromosomal location of a *Triticum dicoccoides*-derived powdery mildew resistance gene in common wheat by using microsatellite markers. Theor Appl Genet 106:341–345

Xue F, Ji W, Wang C, Zhang H, Yang B (2012) High-density mapping and marker development for the powdery mildew resistance gene *PmAS846* derived from wild emmer wheat (*Triticum turgidum* var. *dicoccoides*). Theor Appl Genet 124:1549–1560

Yamamori M (1994) An N-band marker for gene *Lr18* for resistance to leaf rust in wheat. Theor Appl Genet 89:643–646

Yu GT, Zhang Q, Klindworth DL, Friesen TL, Knox R, Jin Y, Zhong S, Cai X, Xu SS (2010) Molecular and cytogenetic characterization of wheat introgression lines carrying the stem rust resistance gene *Sr39*. Crop Sci 50:1393–1400

Yu LX, Barbier H, Rouse MN, Singh S, Singh RP, Bhavani S, Huerta-Espino J, Sorrells ME (2014) A consensus map for Ug99 stem rust resistance loci in wheat. Theor Appl Genet 127:1561–1581

Yu G, Zhang Q, Friesen TL, Rouse MN, Jin Y, Zhong S, Rasmussen JB, Lagudah ES, Xu SS (2015) Identification and mapping of *Sr46* from *Aegilops tauschii* accession CIae 25 conferring resistance to race TTKSK (Ug99) of wheat stem rust pathogen. Theor Appl Genet 128:431–443

Yudina RS, Leonova IN, Salina EA, Khlestkina EK (2015a) Effect of alien genomic introgressions on the osmotic stress resistance of wheat. Russ J Genet Appl Res 5:168–173

Yudina RS, Leonova IN, Salina EA, Khlestkina EK (2015b) Change of salt tolerance in common wheat after introgression of genetic material from *Aegilops speltoides* and *Triticum timopheevii*. Vavilov J Genet Breed 19:171–175

Zegeye H, Rasheed A, Makdis F, Badebo A, Ogbonnaya FC (2014) Genome-wide association mapping for seedling and adult plant resistance to stripe rust in synthetic hexaploid wheat. PLoS ONE 9:e105593

Zeller FJ (1973) 1B/1R wheat-rye chromosome substitutions and translocations. In: Proceedings of 4th international wheat genetic symposium, Mo Agric Exp Stn, Columbia, MO, p 209

Zhang H, Fu H, Ma S (2009) Intraspecific hybridization among *Aegilops tauschii* varieties and genetic analysis and molecular markers of a novel stripe rust resistance gene from *Ae. tauschii*. Chin J Appl Environ Biol 15:44–47

Zhang Q, Klindworth DL, Friesen TL, Chao S, Jin Y, Cai X, Xu SS (2012) Development and characterization of wheat lines with *Sr37* for stem rust resistance derived from wild Timopheev's wheat. In: International conference on "Plant and Animal genome XXI". San Diego, USA, p 316

Zhou JP, Yao CH, Yang EN, Yin MQ, Liu C, Ren ZL (2014) Characterization of a new wheat-*Aegilops biuncialis* addition line conferring quality-associated HMW glutenin subunits. Genet Mol Res 13:660–669