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ORIGINAL PAPER

Comparative mapping of genes for glume colouration and pubescence in hexaploid wheat (*Triticum aestivum* L.)

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Abstract Microsatellite markers were used to map the major genes *Bg* (determining black glume colour), *Rg1* and *Rg3* (red glume), and a locus determining smokey-grey coloured glume to the distal ends of the short arms of the homoeologous group 1 chromosomes, proximally (or closely linked) to *Xgwm1223* and distal to *Xgwm0033*. On this basis, we propose that these genes represent a set of homoeoloci, designated *Rg-A1*, *Rg-B1*, and *Rg-D1*. *Rg3* and *Bg* appear to be variant alleles of *Rg-A1*. Both *Rg3* and *Bg* are closely linked with the major glume pubescence gene *Hg*. Similarly, the hexaploid wheat smokey-grey glume gene and *Rg2* represent alleles at *Rg-D1*. The microsatellite markers linked to the *Rg* genes were used to analyse a phenotypically and genotypically characterized set of Siberian spring wheats. A coincidence between the presence of the 264-bp allele of *Xgwm0136* and *Rg-A1b* (*Rg3*) was observed; so *Xgwm0136* can probably be used as a diagnostic marker for this gene.

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Introduction

Glume colouration and pubescence are important taxonomic discriminators in wheat (Mansfeld 1951; Dorofeev et al. 1979) and are commonly used for the determination of homogeneity within or distinctness between wheat varieties (UPOV 1994). However, they are also known to be associated with the crop's adaptability. In particular, coloured glumes are frequent in varieties adapted to growing regions characterized by high light intensity, as postulated by Flaksberger (1935) and supported by the data of Börner et al. (2005). In addition, glume colouration has a selective advantage in regions characterized both by a short growing season (Börner et al. 2005) and where low temperatures are experienced during the vegetative period (Martynov and Dobrotvorskaya 1997). Glume pubescence appears to have a beneficial influence on drought or cold tolerance (Threthowan et al. 1998; Reynolds et al. 1999; Skovmand et al. 2003; Börner et al. 2005).

The mode of inheritance of glume colour and pubescence has been understood for many years (Tschermak 1901; Biffen 1905), and with the development of wheat aneuploids, the major genes responsible for glume colour and pubescence were located to their respective chromosomes. Thus, red glume colour genes were mapped to chromosome 1B (*Rg1*) of hexaploid wheat (Unrau 1950), to chromosome 1D (*Rg2*) of the synthetic wheat of *Triticum durum* (AABB) × *Aegilops tauschii* (DD) (Kerber and Dyck 1969), and to chromosome 1A (*Rg3*) of hexaploid wheat (Yelokhina 1989; Sobko and Sozinov 1993), while *Bg* (black glume colour) was also mapped to chromosome 1A (Burnham 1962; Law and Chapman 1974). Meanwhile, two genes

responsible for glume pubescence were mapped to chromosomes 1A (*Hg*; Sears 1953) and 1D (*Hg1*; Gulyaeva 1984). Apart from the red and black glume colours, dark-brown and smokey-grey glumes have also been described in hexaploid wheat *Triticum aestivum* (Koval 1994; Pshenichnikova et al. 2005). These are under the control of genes on chromosome 1D, and the smokey-grey colour gene is thought to be an allele of *Rg2* (Pshenichnikova et al. 2005). All these genes (*Rg*, *Bg*, *Hg* and the smokey-grey glume colour gene) are closely linked to their respective gliadin (*Gli-1*) loci (Poperelya et al. 1980; Jones et al. 1990; Sobko and Sozinov 1993, 1997; Panin and Netsvetaev 1986; Khlestkina et al. 2000; Pshenichnikova et al. 2005), establishing their location to the short arms of the homoeologous group 1 chromosomes.

The intra-chromosomal locations of *Bg*, *Hg*, and *Rg1* have been determined in diploid and tetraploid wheats (Dubcovsky and Dvorak 1995; Van Deynze et al. 1995; Blanco et al. 1998; Salina et al. 2006), but not to date in hexaploid wheat. *Rg3* and the smokey-grey colour genes were not mapped. Thus, in the present study, we have exploited relevant microsatellite markers (Röder et al. 1998) for the precise comparative mapping of *Hg*, *Bg*, *Rg1*, *Rg3*, and the smokey-grey glume colour gene in hexaploid wheat. Furthermore, we report the distribution of alleles at microsatellite loci linked to these genes within a phenotypically and genetically characterized set of Siberian spring wheats.

Materials and methods

Plant materials

Five crosses between hexaploid wheat (*T. aestivum* L.) cultivars, lines and accessions were used to create mapping populations (Table 1).

1. Cultivar 'Zhnitsa' (*Rg3/hg*), kindly provided by T.T. Efremova (ICG, Novosibirsk), was crossed with white and hairy glumed wheat accession 'TRI 542' (IPK-Genebank collection).
2. Near-isogenic line 'i:S29BgHg' carrying the dominant alleles of *Bg* and *Hg* introgressed from the black/hairy glumed accession 'k-20551' via the near-isogenic line 'ANK-22A' (Arbuzova et al. 1998) was crossed with white and glabrous glumed wheat accession 'TRI 546' (IPK-Genebank collection).
3. Cultivar 'Federation' (*Rg1*) was crossed with white and glabrous glumed wheat accession 'TRI 546'.

4, 5. Two populations were used for mapping the smokey-grey glume colouration gene: cultivar 'Golubka' (smokey-grey glume) × cultivar 'Novosibirskaya 67' (white glume) and cultivar 'Golubka' (smokey-grey glume) × Kazakstan wheat line 'L301' (white glume).

Table 1 Crosses and population sizes

Cross no.	Cross	Number of F_2 plants/F_3 families	
(1)	'Zhnitsa' × 'TRI 542'	48	F_3 families
(2)	'i:S29BgHg' × 'TRI 546'	97	F_2 plants
(3)	'Federation' × 'TRI 546'	105	F_3 families
(4)	'Golubka' × 'Novosibirskaya 67'	74	F_3 families
(5)	'Golubka' × 'L301'	44	F_2 plants

A collection of Siberian spring wheat cultivars (Table 2), including some with known presence/absence of *Rg* genes (Efremova et al. 1998), was used for phenotyping and microsatellite-based genotyping.

Phenotypic evaluation

Phenotyping was performed at either the F_2 (crosses 2 and 5) or F_3 (crosses 1, 3 and 4) generations. At F_3, 15 individuals per line were evaluated. The population sizes are given in Table 1. The F_1 plants of cross 1 were weak and highly sterile, so only 48 F_2 progeny could be harvested. Plants were scored for glume colour (white, red/brown, black or smokey-grey), and glume pubescence (the latter only in crosses 1 and 2). Glume colour in cross 3 was determined by the segregation of *Rg1*, giving a strong contrast between dark-red and white, while in cross 1, the segregation of *Rg3* resulted in a less clear contrast.

Microsatellite analysis

Leaf material was obtained from F_2 plants of all five mapping populations. DNA was extracted from fresh leaves following a procedure modified from that of Plaschke et al. (1995). Because both the glume colour and pubescence genes are located on the homoeologous group 1 chromosomes, Gatersleben Wheat Microsatellite markers (GWM) mapping to these chromosomes (1A—15 loci; 1B—20 loci; and 1D—13 loci) were selected. The characteristics of all the microsatellites and the experimental procedures associated with their use are described by Röder et al. (1998). Unpublished primer sequences are available upon request. Two additional markers were used for chromosome 1D mapping (*Xbarc149* and *Xbarc152*, Song et al. 2005). Linkage maps were constructed with MAPMAKER 2.0 (Lander et al. 1987). Chromosomal arm positions of

Table 2 Glume colour and microsatellite marker data for a set of Siberian spring wheat cultivars and the parents of the mapping populations (*black rectangle*—'present', *white rectangle*—'absent', *grey rectangle*—'likely present')

Cultivar or accession	White glume	Red glume	Black glume	Smokey-grey glume	*Rg-A1b (Rg3)*	*Xgwm0136*_264bp (1A)	*Xgwm1223*_170bp (1A)	*Rg-B1b (Rg1)*	*Xgwm0033*_120bp (1B)	*Rg-D1c* (smokey-grey)	*Xgwm1223*_165bp (1D)	*Xgwm0337*_185bp (1D)
TRI 546	■											
TRI542	■											
FEDERATION		■						■	■			
ZHNITSA*		■			■	■	■	■				
I:S29BGHG			■									
SYNTHETIC		■										
OPATA 85	■											
GOLUBKA				■						■	■	■
ISKRA*		■			■	■	■					
TCEZIUM 111		■		■				■		▒		■
OMSKAYA 9	■											
OMSKAYA 11	■											■
NOVOSIBIRSKAYA 89	■											
KANTEGIRSKAYA 89	■											
SIBAKOVSKAYA 3	■											
TCELINNAYA 60	■											
SELENGINSKAYA*		■						■				
MILTURUM 2078*		■			■			■				
KRASNOYARSKAYA 1103*		■						■				
SKALA	■											
TARSKAYA 2		■										
PYROTHRIX 28*		■					■	■				
STRELA*		■			■	■	■	■				
ALENKAYA*		■						■				
BALAGANKA *		■						■				
GDS-11		■										
SIBIRKA 1818*		■						■				
IRTYSHANKA 10	■											
SIBIRYACHKA 8	■											
NIVA*		■					■	■				
DUVANKA 501*		■			■	■	■	■				
KROHINSKAYA		■										
POBEDA*		■						■				
TCEZIUM 94		■		■						▒		
NARYMSKAYA 3		■										
NOVOSIBIRSKAYA 22	■											
NARYMSKAYA 246		■										
SIBIRYACHKA 4	■											
LYUTESTCENS 62	■											
AKMOLINKA 1		■										
MILTURUM 553*		■			■	■	■	■				
ALBIDUM 43	■											
SARATOVSKAYA 29	■											
NOVOSIBIRSKAYA 67	■											
IRKUTSKAYA 49	■										■	■
LYUTESTCENS 116	■										■	■
ALBIDUM 3700	■											■
SARATOVSKAYA 36	■											
SARATOVSKAYA 39	■											
ALTAISKAYA 50	■											
ALTAISKAYA 60	■											
ALTAISKAYA 98	■											
ALTAISKII PROSTOR	■											

* Genes controlling glume colour of these cultivars were determined by Efremova et al. (1998)

loci mapped in the centromeric region were confirmed by the analysis of the relevant ditelosomic lines of 'Chinese Spring'. Selected markers linked to the *Rg* genes (1A—*Xgwm0136*; 1A, 1B, 1D—*Xgwm0033*; 1A, 1D—*Xgwm1223*; 1D—*Xgwm0337*) were used for the genotypic analysis of the Siberian spring wheat collection.

Results

Chromosome 1A mapping

Among the F_3 families from cross 1, 8 were homozygous red, 28 heterozygous and 12 homozygous white, consistent with a monogenic 1:2:1 segregation ($\chi^2 = 2.00$, $P > 0.30$). In the F_2 from cross 2, 79 individuals had black glumes, and 18 were white, fitting a monogenic 3:1 segregation ratio ($\chi^2 = 2.15$, $P > 0.10$). Both red and black glume colouration were dominant over white. Additionally, both populations segregated for glume pubescence (*Hg*). There was no recombination either between *Rg3* and *Hg* in cross 1, or between *Bg* and *Hg* in cross 2. Of the fifteen 1A microsatellite markers tested, ten were polymorphic between the parents of cross 1 (67%) and nine of cross 2 (60%), and could therefore be genetically mapped (Fig. 1). Both *Rg3* and *Bg* map to the distal end of chromosome 1AS, closely linked to *Xgwm1223* (0.0 and 0.6 cM, respectively) and distal to *Xgwm0136* (4.7 cM from *Rg3*) and *Xgwm0033* (4.6 cM from *Bg*). The highly similar intrachromosomal positions of *Rg3* and *Bg* loci is established by seven markers common to both maps.

Chromosome 1B mapping

In the F_3 from cross 3, a segregation of 25 homozygous red glumes, 59 heterozygous and 21 homozygous white was observed. This is consistent with the presence of a monogenic dominant gene ($\chi^2 = 1.90$, $P > 0.30$). Of the 20 chromosome 1B microsatellite markers tested, 15 (75%) were polymorphic between the parents of the cross, allowing the mapping of *Rg1* to the distal end of chromosome 1BS, proximal to *Xgwm1078* (4.2 cM) and distal to *Xgwm0550* (3.1 cM) and *Xgwm0033* (6.5 cM) (Fig. 1).

Chromosome 1D mapping

The F_3 of cross 4 produced 43 lines homozygous for smokey-grey glumes, 22 heterozygous and 9 homozygous white, which does not fit the expected 1:2:1 ratio ($\chi^2 = 43.41$, $P < 0.01$). Of the 15 chromosome 1D microsatellites tested, 9 (60%) were polymorphic between the parents, but the pattern of segregation of all these loci was distorted. For this reason, a second cross involving 'Golubka', the source of the smokey-grey glumes, was investigated (cross 5). In this case, the smokey-grey glume locus segregated consistently with a 3:1 ratio ($\chi^2 = 0.121$, $P > 0.70$), and the segregation pattern of the microsatellite loci was not distorted. Linkage maps of chromosome 1D were obtained using both populations 4 and 5 involving, respectively, nine and three microsatellite loci (Fig. 1). The smokey-grey glume locus mapped to the distal end of chromosome 1DS, closely linked to *Xgwm1223* (1.5 cM) and distal to *Xbarc152* (13.1 cM).

Identification of diagnostic markers

The germplasm set (53 entries, including the Siberian spring wheat collection and the parents of the mapping populations, Table 2), were genotyped at loci

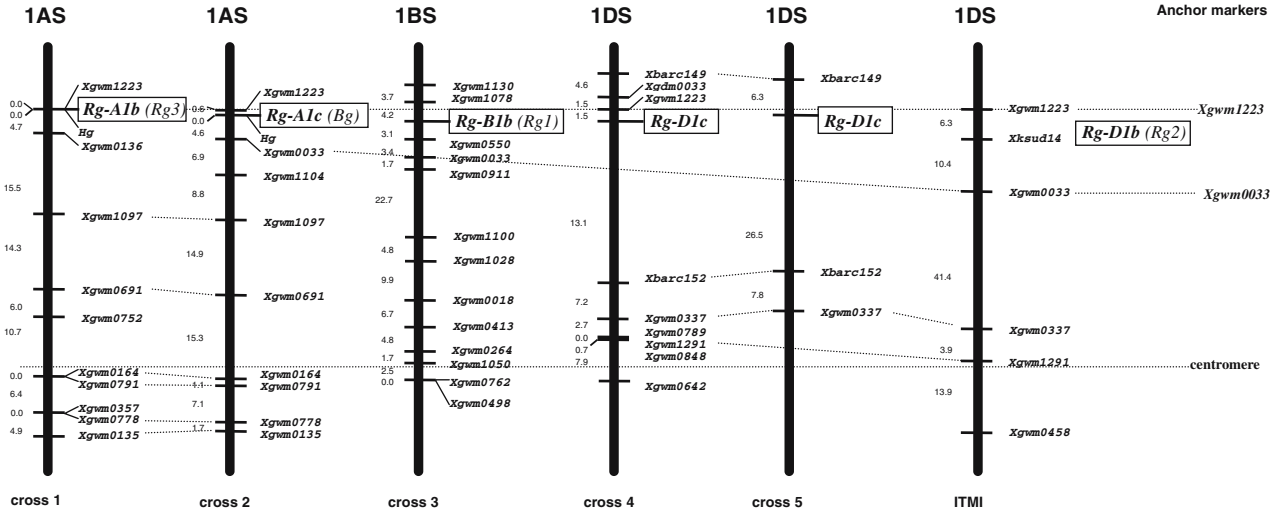

Fig. 1 Comparative mapping of the genes for glume colouration and pubescence in hexaploid wheat using microsatellite markers. Chromosome designations are indicated above. Genetic distances are given in centimorgans (cM). Crosses for mapping populations are indicated below. The maps were constructed with the MAPMAKER 2.0 computer program (adapted from Lander et al. 1987). Map of 1DS chromosome in ITMI population was obtained from Börner et al. (2002) and Röder et al. (1998)

Xgwm0136 (1A), *Xgwm0033* (1A, 1B, 1D), *Xgwm1223* (1A, 1D), and *Xgwm0337* (1D). These markers were selected as they amplify characteristic alleles among the mapping parents, namely *Xgwm0136*_264 ('Zhnitsa', *Rg3*), *Xgwm0033*_120 ('Federation', *Rg1*), *Xgwm1223*_170 ('Zhnitsa', *Rg3*) and _165 ('Golubka', smokey-grey glume), and *Xgwm0337*_185 bp ('Golubka'). The resulting genotypic data were matched with the *Rg* classifications of Efremova et al. (1998) and/or with the phenotypic data obtained in the present study. No coincidence was found between characteristic microsatellite alleles and the presence of a particular glume colour gene for either *Xgwm0033*, *Xgwm1223* or *Xgwm0337* (Table 2). However, the 264 bp allele of *Xgwm0136* was amplified in five entries (cultivars 'Strela', 'Duvanka 501', 'Milturum 553', 'Iskra', 'Zhnitsa') known to carry *Rg3* (Efremova et al. 1998), while all entries lacking *Rg3* did not amplify this allele. The presence of one exception ('Milturum 2078', see Table 2) may be explained by recombination between *Rg3* and *Xgwm0136* (4.7 cM, see Fig. 1).

Discussion

DNA markers have facilitated the precise mapping of several sets of wheat genes, and this has provided good support for the existence of homoeologous series. For instance, homoeologous sets have been defined for red grain colour (*R*) (Flintham and Gale 1995), photoperiodic response (*Ppd*) and vernalization sensitivity (*Vrn*) (Börner et al. 1998), sphaerococcoid spike morphology (*S*) and anthocyanin colouration of coleoptiles (*Rc*) (Salina et al. 2000; Khlestkina et al. 2002) and awn colour (*Bla*) (Börner et al. 2002). The homoeoloci determining glume colouration each map towards the end of the 1S chromosome arms, distal to *Xgwm0033* but proximal (or closely linked) to *Xgwm1223*. The map positions of *Bg* and *Rg3* on chromosome 1AS are very similar (Fig. 1), and both *Rg3* and *Bg* are closely linked to *Hg*. Whereas the dominant *Rg3* allele was linked with the recessive one at *Hg*, both *Bg* and *Hg* are dominant. The strong associations *Bg*/*Hg* and *Rg3*/*hg* have been noted earlier (Philipchenko 1934; Sobko and Sozinov 1997; Efremova et al. 1998).

Arbuzova et al. (1995) and Sobko and Sozinov (1997) have suggested that black and red glume colouration are controlled by different genetic systems on chromosome 1A. However, considering the close linkage of both *Bg* and *Rg3* with *Hg*, and on the basis of the comparable map positions of these genes, we suggest in contrast that *Bg* and *Rg3* represent alleles of the same gene. Likewise, we have observed similar mapping positions for the smokey-grey glume colouration gene and *Rg2* (Börner et al. 2002) on chromosome 1DS, which led to the suggestion that they are allelic forms (Pshenichnikova et al. 2005). Unlike *Rg2* which originates from the diploid donor *Ae. tauschii*, the smokey-grey glume allele of 'Golubka' arose in common wheat, as far as is known, since the pedigree records for this cultivar show that it was a selection from a cross between spring bread wheats, made in the USSR in 1933 (Guidebook 1947). Thus, we believe that *Bg* (1A), *Rg3* (1A), *Rg1* (1B), *Rg2* (1D), and the gene determining smokey-grey glume colouration (1D) represent allelic variants at a set of homoeoloci, and therefore propose a change in their designation to *Rg-A1*, *Rg-B1* and *Rg-D1*, with *Rg-A1a*, *Rg-B1a* and *Rg-D1a* representing the non-coloured alleles. Following this new designation, the red and black colour alleles at *Rg-A1* become *Rg-A1b* and *Rg-A1c*, respectively, and *Rg2* and the smokey-grey glume genes become *Rg-D1b* and *Rg-D1c*, respectively.

The coincidence between the *Xgwm0136*_264 allele and *Rg-A1b* provides a further example of the utilization of microsatellites as diagnostic markers, first demonstrated by Worland et al. (1998) for *Xgwm261* and the dwarfing gene *Rht8*. A more recent example of this approach was provided by the report of Khlestkina et al. (2006) of an association between *Xgwm0533* and an adult plant resistance gene against yellow rust (*Yrns-B1*). *Rg* and *Hg* have potential as morphological markers for disease resistance selection, since a number of major fungal resistance genes (*Lr10* and *Pm3* on 1AS, *Yr10* on 1BS, *Lr21* on 1DS) are known to map to this region of the genome (McIntosh et al. 2003).

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References

Arbuzova VS, Efremova TT, Laikova LI, Maystrenko OI, Popova OM, Pshenichnikova TA (1995) The main results of the study of developing aneuploid and substitution lines and genetic analysis of wheat. EWAC Newsl 9:116–117

Arbuzova VS, Maystrenko OI, Popova OM (1998) Development of near-isogenic lines of the common wheat cultivar 'Saratovskaya 29'. Cereal Res Commun 26:39–46

Biffen RH (1905) Mendel's law of inheritance and wheat breeding. J Agric Sci 1:48

Blanco A, Bellomo MP, Cenci A, De Giovanni C, D'Ovidio R, Iacono E, Laddomada B, Pagnotta MA, Porceddu E, Sciancalepore A, Simeone R, Tanzarella OA (1998) A genetic linkage map of durum wheat. Theor Appl Genet 97:721–728

Börner A, Korzun V, Worland AJ (1998) Comparative genetic mapping of mutant loci affecting plant height and development in cereals. Euphytica 100:245–248

Börner A, Schumann E, Fürste A, Cöster H, Leithold B, Röder MS, Weber WE (2002) Mapping of quantitative trait loci determining agronomic important characters in hexaploid wheat (*Triticum aestivum* L.). Theor Appl Genet 105:921–936

Börner A, Schäfer M, Schmidt A, Grau M, Vorwald J (2005) Associations between geographical origin and morphological characters in bread wheat. Plant Genet Resour 3:360–372

Burnham CR (1962) Discussions in cytogenetics. Burgess Publishing Co., Minneapolis, pp 1–375

Dorofeev VF, Filatenko AA, Migushova EF, Udachin RA, Jacubziner MM (1979) Flora of cultivated plants. Kolos, Leningrad, 348 p (in Russian)

Dubcovsky J, Dvorak J (1995) Ribosomal RNA multigene loci: nomads of the *Triticeae* genomes. Genetics 140:1367–1377

Efremova TT, Maystrenko OI, Arbuzova VS, Laikova LI (1998) Genetic analysis of glume colour in common wheat cultivars from the former USSR. Euphytica 102:211–218

Flaksberger KA (1935) Wheat. In: Wulff EV (ed) Flora of cultivated plants (in Russian). State Agricultural Publishing Company, Leningrad, Moscow, pp 1–434

Flintham JE, Gale MD (1995) Dormancy gene maps in homoeologous cereal genomes. In: Proceedings of the 7th international symposium on pre-harvest sprouting in cereals, pp 143–149

Guidebook on Crop Approbation: Grain Crops (1947) In: Yakubtsiner MM, Savitsky MS (eds) OGIZ-Sel'khozgiz, Moscow, 639 p (in Russian)

Gulyaeva ZB (1984) Localization of the genes for pubesence of the glumes and coloration of the auricles in the leaf sheath in winter wheat variety Ulyanovka (in Russian). Trudy po Prikladnoi Botanike, Genetike i Selektsii 85:95–96

Jones SS, Dvorak J, Qualset CO (1990) Linkage relations of *Gli-D1*, *Rg2*, and *Lr21* on the short arm of chromosome 1D in wheat. Genome 33:937–940

Kerber ER, Dyck PL (1969) Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from *Aegilops squarrosa*. Can J Genet Cytol 11:639–647

Khlestkina EK, Salina EA, Pshenichnikova TA, Arbuzova VS, Koval' SF (2000) Analysis of isogenic lines of the soft wheat carrying dominant alleles of *Bg*, *Hg*, and *Rg1* genes using microsatellite and protein markers. Russ J Genet 36:1153–1158

Khlestkina EK, Pestsova EG, Röder MS, Börner A (2002) Molecular mapping, phenotypic expression and geographical distribution of genes determining anthocyanin pigmentation of coleoptiles in wheat (*Triticum aestivum* L.). Theor Appl Genet 104:632–637

Khlestkina EK, Röder MS, Unger O, Meinel A, Börner A (2006) More precise map position and origin of a durable non-specific adult plant disease resistance against stripe rust (*Puccinia striiformis*) in wheat. Euphytica (in press)

Koval SF (1994) Genetic analysis of isogenic lines of spring wheat variety Novosibirskaya 67: 1. Location of the gene determining the brown color of the glume in chromosome 1D. Russ J Genet 30:508–509

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg I (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Law CN, Chapman V (1974) An inhibitor of glume colour. EWAC Newsl 4:8–9

Mansfeld R (1951) Das morphologische System des Saatweizens, *Triticum aestivum* L.s.l. Der Züchter 21:41–60

Martynov SP, Dobrotvorskaya TV (1997) Distribution characteristics of traits ear morphology in common wheat in the former Soviet Union. Russ J Genet 33:350–357

McIntosh RA, Yamazak Y, Devos KM, Dubcovsky J, Rogers J, Appels R (2003) Catalogue of gene symbols for wheat. http://www.grs.nig.ac.jp/wheat/komugi/genes/

Panin VM, Netsvetaev VP (1986) Genetic control of gliadins and some morphological characters of spike in durum winter wheats (in Russian). Nauchno-Tekhnicheskii Bull. VSG I. Odessa 2:31–36

Philipchenko YuA (1934) Genetics of soft wheats. OGIZ-Sel'khozgiz, Leningrad, Moscow, pp 1–262

Plaschke J, Ganal MW, Röder MS (1995) Detection of genetic diversity in closely related bread wheat using microsatellite markers. Theor Appl Genet 91:1001–1007

Poperelya FA, Bito M, Sozinov AA (1980) Relation of gliadin component clusters to plant survival and productivity, glume color, and flour quality in F_2 hybrids between cultivars Bezostaya and Cervena Zvezda (in Russian). Doklady VASKHNIL 4:4–7

Pshenichnikova TA, Bokarev IE, Shchukina LV (2005) Hybrid and monosomic analyses of smoky coloration of the ear in common wheat. Russ J Genet 41:1147–1149

Reynolds M, Skovmand B, Threthowan RM, Pfeiffer W (1999) Evaluating a conceptual model of drought tolerance. In: Ribaut JM (ed) Using molecular markers to improve drought tolerance. CIMMYT, Mexico, pp 49–53

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier M-H, Leroy P, Ganal MW (1998) A microsatellite map of wheat. Genetics 149:2007–2023

Salina E, Börner A, Leonova I, Korzun V, Laikova L, Maystrenko O, Röder MS (2000) Microsatellite mapping of the induced sphaerococcoid mutation genes in *Triticum aestivum*. Theor Appl Genet 100:686–689

Salina EA, Leonova IN, Efremova TT, Röder MS (2006) Wheat genome structure: translocations during the course of polyploidization. Funct Integr Genomics 6:71–80

Skovmand B, Reynolds M, Lage J (2003) Collecting and managing wheat genetic resources and exploiting germplasm collections to find useful traits. Abstract 11th Central Asian wheat conference. Almaty, 2003, 389 p

Sears ER (1953) Nullisomic analysis in common wheat. Am Nat 87:245–252

Sobko TA, Sozinov AA (1993) Genetic control of morphologic traits of a spike and the relationship with allelic variation of marker loci of chromosomes 1A and 1B of winter common wheat. Tsitol Genet 27:15–22

Sobko TA, Sozinov AA (1997) Linkage mapping of the loci controlling spike morphological traits and seed storage proteins on the 1A chromosome in winter common wheats. Tsitol Genet 31:18–26

Song QJ, Shi JR, Singh S, Fickus EW, Costa JM, Lewis J, Gill BS, Ward R, Cregan PB (2005) Development and mapping of microsatellite (SSR) markers in wheat. Theor Appl Genet 110:550–560

Threthowan RM, Reynolds MP, Skovmand B, van Ginkel M (1998) The effect of glume pubescence on floret temperature in wheat. Agronomy Abstracts, Baltimore, 161 p

Tschermak E (1901) Über Züchtung neuer Getreiderassen mittelst künstlicher Kreuzung. Zts Landw Versuchsw, Oesterreich 4:1029–1060

Unrau J (1950) The use of monosomes and nullisomes in cytogenetic studies in common wheat. Sci Agric 30:66–89

UPOV (1994) Guidelines for the conduct of tests for distinctness, uniformity and stability. International union for the protection of new varieties, pp 1–34

Van Deynze AE, Dubcovsky J, Gill KS, Nelson JC, Sorrells ME, Dvorak J, Gill BS, Lagudah ES, McCouch SR, Appels R (1995) Molecular-genetic maps for group 1 chromosomes of *Triticeae* species and their relation to chromosomes in rice and oat. Genome 38:45–59

Worland AJ, Korzun V, Röder MS, Ganal MW, Law CN (1998) Genetic analysis of the dwarfing gene *Rht8* in wheat. Part II. The distribution and adaptive significance of allelic variants at the *Rht8* locus of wheat as revealed by microsatellite screening. Theor Appl Genet 96:1110–1120

Yelokhina LP (1989) Genetic control of spike coloration in the common spring wheat cv. 'Milturum 553'. Proc Conf Sci Advanc Agric, Omsk 1:13–14