

GENETIC COLLECTION AND DEVELOPMENT OF NEAR-ISOGENIC LINES IN DURUM WHEAT

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Genetic collections of tetraploid and hexaploid wheats were utilized to develop near-isogenic lines in durum wheat. The genes to be introduced were located on the specific chromosome and mapped to linkage maps using aneuploid stocks of LD222 and Langdon, Landgdon D-genome chromosome substitution lines, and microsatellite markers. We contributed mapping of the genes for long glumes on chromosomes 7AL and 7BL, genes for brittle rachis on chromosomes 3AS and 3BS and the gene for ligulelessness on chromosome 2BL. The mutant gene for sphaerococcoid grain, *s*¹⁶²¹⁹, was allelic to *S2*, which was located on the centromeric region of chromosome 3B in hexaploid wheat. The gene for compact spike, *C*¹⁷⁶⁴⁸ was located on the chromosome 5AL. Near-isogenic lines were developed for the GA-sensitive *Rht* genes, *Rht14*, *Rht16* and *Rht18*, on chromosome 6AS. The multiple alleles at the *Rht-B1* locus were introduced to cv. LD222. *Triticum polonicum* IC 12196 may be considered as new source of reduced height genes. Forty-one near-isogenic lines were developed. Twenty-nine donors of genes were from tetraploid wheat collection for near-isogenic lines, and 12 were from hexaploid wheat accessions for near-isogenic lines. The effort to develop near-isogenic lines was extended to introduce taxonomy-related traits such as spelt and awn on the glumes.

Key words: genetic collections, *Triticum durum*, near-isogenic lines, mutes, morphological traits.

Introduction

It is usually difficult to precisely determine the effects of specific genes on the plant performance, because these effects are usually limited and often influenced by the environment in which the plants are grown. However, these effects can be determined accurately using isogenic lines, which are not usually available in tetraploid wheat and it takes time to develop them. It is necessary to create the primary genetic collection and to study inheritance of individual traits for development of near-isogenic lines. In comparison with hexaploid wheat species, aneuploid analysis was not applied in tetraploid wheat until Joppa, Williams (1988) who made Langdon durum substitution lines. The establishment of a genetic collection in tetraploid wheat was restricted because the knowledge of inheritance of specific characters was scarce. Hence, the utilization of genetic collections of hexaploid wheat may be beneficial.

To develop near-isogenic lines in tetraploid wheat, the genes to be introduced were located on a specific

chromosome using aneuploid stocks of LD222 (Nishikawa, unpublished) and Langdon (Joppa, 1993), Landgdon D-genome chromosome substitution lines (Joppa, Williams, 1988). The linkage maps of these genes were developed using microsatellite markers (Röder *et al.*, 1998; Song *et al.*, 2005; Torada *et al.*, 2006). Simultaneously, the author incorporated several major genes into the genetic background of the spring durum wheat cultivar LD222. The author also paid attention to apply duplicate donors for the same traits, and to incorporate homoeologous loci and multiple alleles.

Materials and Methods

Genetic collection. The author assembled the mutants of durum wheat, such as sphaerococcoid mutant (Schmidt, Johnson, 1963) and chlorina mutants (Klindworth *et al.*, 1995), tetraploid wheat accessions whose characters were controlled by homoeologous genes, and accessions with key characters for botanical classification of tetraploid wheat species. The elongated glume character

from *Triticum polonicum* and *T. ispahanicum*, *tetraaristatus* (awn on the inner and outer glumes) trait from *T. carthlicum* and the branched spike trait from *T. turgidum* were considered. The chromosome substitution lines of Langdon-*T. dicoccoides* (Joppa, Cantrell, 1990) were also utilized. These accessions were used to incorporate the genes into *T. durum* cv. LD222.

Development of near-isogenic lines. A line of spring durum wheat, LD222 was used as a recurrent parent. The basic method to develop near-isogenic line was described in Watanabe (1994). The F₁ hybrids of LD222 and the donors were backcrossed with LD222. In each backcross generation, ten plants were grown to confirm the segregation ratio of 1 : 1 and to select heterozygous plants for dominant characters. The heterozygous plant was crossed with LD222 in each backcross generation. After six backcrosses, heterozygous B₆F₁ plants were selfed, and then homozygous plants with dominant characters were recovered from the B₆F₄ generation. For the recessive traits, the plants were selfed to confirm the presence of recessive trait, and the plants with recessive trait in the later generation were crossed with LD222.

The recombination, allelic relationship and mapping of genes to chromosomes. The genes to be introduced are located on the specific chromosome and mapped in the linkage maps using the aneuploid stocks and microsatellite markers. The linkage map and allelic relationship among genes were also considered.

Microsatellite mapping. Genomic DNA was extracted from seedling leaves from the individuals per F₂ populations according to Dellaporta *et al.* (1983). To map the genes we used the wheat *Xgwm*, *Xbarc* and *Xhbg* microsatellite markers. *Xgwm*, *Xbarc* and *Xhbg* microsatellite markers were available from Röder *et al.* (1998), Song *et al.* (2005) and Torada *et al.* (2006), respectively. PCR conditions were as followings (10 µl total volume): 1 µl of 1 × Standard Taq Reaction Buffer (New England BioLab. Inc.), 1 µl of 2 mM dNTPs, 0.96 µl of 37 % glycerol solution (w/w), 0.04 µl of Taq DNA Polymerase (5 units/ml; New England BioLab. Inc.), 2 µl of template DNA (50 ng/µl), 3 µl of the mixture of 0.2 µM each of the forward and reverse primers and 2 µl of sdH20. Amplification was carried out on a GeneAmp® PCR System 2700 (Applied Biosystems) running the following

program: 2 min at 94 °C; seven “touchdown” cycles of 15 s at 94 °C, 30 s at 63 °C, 15 s at 68 °C with a 1 °C drop in annealing temperature at each cycle; then 35 cycles of 15 s at 94 °C, 30 s at 55 °C, 15 s at 68 °C. Electrophoresis of PCR products was done in 10 % acrylamide gel at constant voltage (300 V). The running buffer used was 0.15 M Tris-Glycine (pH 8.8). Amplified fragments were detected by silver staining. Multipoint linkage values in centiMorgans (cM) were calculated using Map Manager QTX (<http://mapmgr.roswellpark.org/>). Minimum LOD scores of > 3.0 were used to develop the linkage map. The software calculated genetic distances in centiMorgans (cM) by applying the Kosambi (1944) mapping function.

Results

Table 1 shows the genetic collection and chromosomal location of the genes which were utilized to develop near-isogenic lines. The genes for black glume were closely linked with those for hairy glume and they were located on the distal part of chromosome 1AS. The genes for ligulelessness and non-glaucousness were located on the distal part of long and short arm of chromosome 2B, respectively. Although it was supposed that another recessive gene on chromosome 2A is necessary to determine the liguleless trait, the author did not find it in the genetic collection. Kosuge *et al.* (2008) confirmed that the mutant gene for sphaerococcoid grain, *s¹⁶²¹⁹*, was allelic to *S2*, which is located on the centromeric region of chromosome 3B in hexaploid wheat. Homoeologous gene *S3* on chromosome 3A was introduced from a hexaploid accession (Salina *et al.*, 2000) to LD222. The author found the homoeologous genes on group 3 chromosomes determined brittle rachis and red grains. The genes for brittle rachis were located using aneuploid stocks and microsatellite markers (Table 1).

Although homoeologous genes for blue grain have been found, it was difficult to introduce the gene on chromosome 4A from diploid species *Triticum boeoticum*. The blue grain gene on chromosome 4B was introduced from an alien introgression hexaploid line, UC66049 (Qualset *et al.*, 2005). The allelic variations in *Rht-B1* locus on chromosome 4B are contained in widely utilized semi-dwarf wheat cultivars (Worland, Sayers, 1995; Börner *et al.*, 1996). As shown in

Table 1

The genetic collections used as the donors to develop near-isogenic lines of LD222

Trait	Chromosomal location and donor		Reference
	A genome	B genome	
Black glume, hairy glume	1AS, <i>T. carthlicum</i> #521	–	Unpublished
Ligulelessness	–	2BL, <i>T. durum</i> k17769	Watanabe <i>et al.</i> , 2004
Non-glaucousness	–	2BS, <i>T. durum</i> k523	Unpublished
Spherical grain	3A, MS 1453	3B, MA16219, a mutant of <i>T. durum</i> cv. Altaiskaya Niva 3B, MSK 2454, a mutant of <i>T. aestivum</i> cv. Skala	Kosuge <i>et al.</i> , 2008 for MA16219, unpublished for MSK 2454
Brittle rachis	3AS, LDN (DIC 3A)	3BS, LDN(DIC 3B)	Watanabe, Ikebata, 2000; Watanabe, Imamura, 2002; Watanabe <i>et al.</i> , 2002b, 2005, 2006
Red grain	3AL, LDN (DIC 3A)	3BL, LDN (DIC 3B)	Watanabe, Ikebata, 2000
Blue grain	–	4BS, UC66049	Unpublished
Compact spike	5AL, MA17648, a mutant of <i>T. durum</i> Altaiskaya Niva	–	Kosuge <i>et al.</i> , 2008
Reduced height, GA-sensitive	6AS, <i>T. durum</i> Castelporziano, Edmore M1, Icaro	–	Present paper
Purple culm	–	7BS, CS (Hope 7B)	Unpublished
Chocolate black chaff	–	7BS, Vic CBC mutant	Watanabe, 1999
Chlorina	7AL, CDd6 mutant	7BL, CDd2 mutant	Klindworth <i>et al.</i> , 1997; Watanabe <i>et al.</i> , 1996; Watanabe, 1999
Long glume	7AL, <i>T. polonicum</i> #518	7BL, <i>T. ispahanicum</i> CL1120001	Watanabe <i>et al.</i> , 1996; Watanabe, 1999; Watanabe, Imamura, 2002; Watanabe <i>et al.</i> , 2002a

Table 2, we introduced seven multiple alleles to LD222. They differed in plant height, number of tillers, spike length and seed dormancy. *Triticum polonicum* IC 12196 may be considered as a new source of variation for semi-dwarfness (Watanabe, 2004). The assessments of characteristics of these near-isogenic lines are being progressed. The *Rht-B1b* allele reduced plant height and caused deep seed dormancy most severely, whereas *Rht-B1c* allele resulted weak, less number of tillers at the early stage of growing. The effects of other alleles

were similar to that of *Rht-B1b* (unpublished results).

Kosuge *et al.* (2008) found that the gene for compact spike, *C¹⁷⁶⁴⁸* was located on the chromosome 5AL. It should be noted that the gibberellic acid sensitively reduced height genes, *Rht14*, *Rht16* and *Rht18*, were induced independently. Castelporziano (*Rht14*) is a mutant of Cappeli. Edmore M1 (*Rht16*) was a mutant of Edmore. Icaro (*Rht18*) was derived from Anhinga. These genes were allelic to each other, and linked with

Table 2

Near-isogenic lines of durum wheat cultivar LD222

Chromosome	Code	Character	Allele	Donor	Source of donor
1	2	3	4	5	6
Chromosome 1A	ANW 1A	Black glume, hairy glume	<i>Bg, Hg</i>	<i>T. durum</i> var. <i>reichenbachii</i>	Gifu University, Japan
	ANW 1B	Black glume, hairy glume	<i>Bg, Hg</i>	<i>T. carthlicum</i> #521	Gifu University, Japan
	ANW 2A	Hairy glume	<i>Hg</i>	<i>T. durum</i> var. <i>melanopus</i> #513	Gifu University, Japan
	ANW 3A	Nonglauousness	<i>W11</i>	<i>T. durum</i> var. <i>pyramidale</i> #523	Gifu University, Japan
	ANW 3B	Nonglauousness	<i>w1</i>	AUS 2499	AWCC, Tamworth, Australia
	ANW 12A	Ligulelessness	<i>lg1</i>	A variant of cv. Marvroullos	Institute of Cytology and Genetics, SB RAS, Novosibirsk, Russia
Chromosome 3A	ANW 9A	Red grain	<i>R-A1b</i>	LDN (DIC 3A)	L.R. Joppa, USDA-ARS, North Dakota, USA
	ANW 10A	Brittle rachis	<i>Br2</i>	LDN (DIC 3A)	L.R. Joppa, USDA-ARS, North Dakota, USA
Chromosome 3B	ANW 11B	Sphaerococcoid	<i>S3</i>	MS 1453, a mutant of cv. Saratovskaya 29 (2n = 42)	ANIISKH, SB RAAS, Barnaul, Russia
	ANW 9B	Red grain	<i>R-B1b</i>	LDN (DIC 3B)	L.R. Joppa, USDA-ARS, North Dakota, USA
	ANW 10B	Brittle rachis	<i>Br3</i>	LDN (DIC 3B)	L.R. Joppa, USDA-ARS, North Dakota, USA
	ANW 11C	Sphaerococcoid	<i>S2</i>	MSK 2454, a mutant of <i>T. aestivum</i> cv. Skala (2n = 42)	ANIISKH, SB RAASs, Barnaul, Russia
	ANW 11D	Sphaerococcoid	<i>S^{1/6219}</i>	MA-16219, a mutant of <i>T. durum</i> cv. Altaiskaya Niva	ANIISKH, SB RAAS, Barnaul, Russia
	ANW 4A	Reduced height	<i>Rht-B1b</i>	<i>T. durum</i> cv. Cando C1tr17438	NSGC, Aberdeen, Idaho, USA
Chromosome 4B	ANW 4B	Reduced height	<i>Rht-B1c</i>	ANIL of <i>T. aestivum</i> cv. Maringa (2n = 42)	John Inne Centre, Norwich, UK
	ANW 4C	Reduced height	<i>Rht-B1d</i>	<i>T. aestivum</i> cv. Saitama 27	John Innes Centre, Norwich, UK
	ANW 4D	Reduced height	<i>Rht-B1e</i>	<i>T. aestivum</i> cv. Krasnodari Karlik1	A. Börner IPK-Gatersleben, Germany
	ANW 4E	Reduced height	<i>Rht-B1f</i>	<i>T. aethiopicum</i> W6824D	A. Börner IPK-Gatersleben, Germany
	ANW 4F	Reduced height	<i>Rht-B1h</i>	<i>T. polonicum</i> IC 12196	ICARDA, Aleppo, Syria

1	2	3	4	5	6
Chromosome 5A	ANW 4G	Reduced height	<i>Rht-B1f</i>	<i>T. aethiopicum</i> W6807C	A. Börner IPK-Gatersleben, Germany
	ANW 16H	Reduced height	<i>Rht 19</i>	<i>T. durum</i> Vic SD1 line b	NSGC, Aberdeen, Idaho, USA
	ANW 14A	Hairy peduncle	<i>Hp</i>	Hp-S615, an S615 NIL (2n = 42)	K. Tsunewaki, Kyoto University, Kyoto, Japan
	ANW 20A	Blue grain	<i>Ba2</i>	UC66049	C.O. Qualset, University of California, Davis, USA
	ANW 16C	Reduced height	<i>Rht 12</i>	Mv 17 (Karcagi 522 5A) (2n = 42)	J. Sutka, Agricultural Research Institute of the Hungarian Academy of Sciences, Martonvásár, Hungary
	ANW 22A	Compact spike	<i>C¹⁷⁶⁴⁸</i>	MA17648, a mutant of Altaiskaya Niva	ANIISKH, SB RAAS, Barnaul, Russia
Chromosome 6A	ANW 16D	Reduced height	<i>Rht 14</i>	<i>T. durum</i> cv. Castelporziano PI 347731	NSGC, Aberdeen, Idaho, USA
	ANW 16F	Reduced height	<i>Rht 16</i>	<i>T. durum</i> cv. Edmore M1 PI 499362	NSGC, Aberdeen, Idaho, USA
	ANW 16G	Reduced height	<i>Rht 18</i>	<i>T. durum</i> cv. Icaro PI 503555	NSGC, Aberdeen, Idaho, USA
Chromosome 7A	ANW 5A	Long glume	<i>PI</i>	<i>T. polonicum</i> var. <i>vestitum</i> #518	Gifu University, Japan
	ANW 5C	Long glume	<i>PI</i>	<i>T. petropavlovskiyi</i> Maystrenko's line (2n = 42)	Institute of Cytology and Genetics, SB RAS, Novosibirsk, Russia
	ANW 5D	Long glume	<i>PI</i>	<i>T. polonicum</i> var. <i>abyssinicum</i>	Gifu University, Japan
	ANW 5E	Long glume	<i>PI</i>	<i>T. petropavlovskiyi</i> K44126 (2n = 42)	Institute of Cytology and Genetics, SB RAS, Novosibirsk, Russia
	ANW 5F	Long glume	<i>PI</i>	<i>T. aestivum aestivum</i> PI 191834	NSGC, Aberdeen, Idaho, USA
Chromosome 7B	ANW 5G	Long glume	<i>PI</i>	<i>T. aestivum</i> AUS 20561	AWCC, Tamworth, Australia
	ANW 7A	Chlorina	<i>cn-A1d</i>	CDd6, a mutant of Langdon	N. D. Williams, USDA-ARS, North Dakota, USA
	ANW 5B	Long glume	<i>P2</i>	<i>T. ispananicum</i> CL1120001	John Innes Centre, Norwich, UK
	ANW 7B	Chlorina	<i>cn-B1b</i>	CDd2, a mutant of Langdon	N. D. Williams, USDA-ARS, North Dakota, USA
	ANW 6A	Purple culm	<i>Pc</i>	CS(Hope 7B)	N. D. Williams, USDA-ARS, North Dakota, USA
	ANW 13A	Chocolate black chaff	<i>cc</i>	Vic CBC mutant	N. D. Williams, USDA-ARS, North Dakota, USA
	ANW 8A	Yellow leaf	(digenic)	<i>T. durum</i> Yellow mutant	John Innes Centre, Norwich, UK
Unknown	ANW 11A	sphaerococcoid	(digenic)	Schmidt's sphaerococcoid mutant	Gifu University, Japan; Schmidt, Johnson (1963)

Note: ANIISKH : Altai Research Institute of Agriculture, SB RAAS, Barnaul, Russia. AWCC: Australian Winter Cereal Collection, Tamworth, Australia, ICARDA: International Center for Agricultural Research Center in the Dry Areas NSGC: National Small Grain Collections, Aberdeen, Idaho, USA.

Castelporziano / LD222 F₂ Edmore M1 / LD222 F₂ Icaro / LD222 F₂

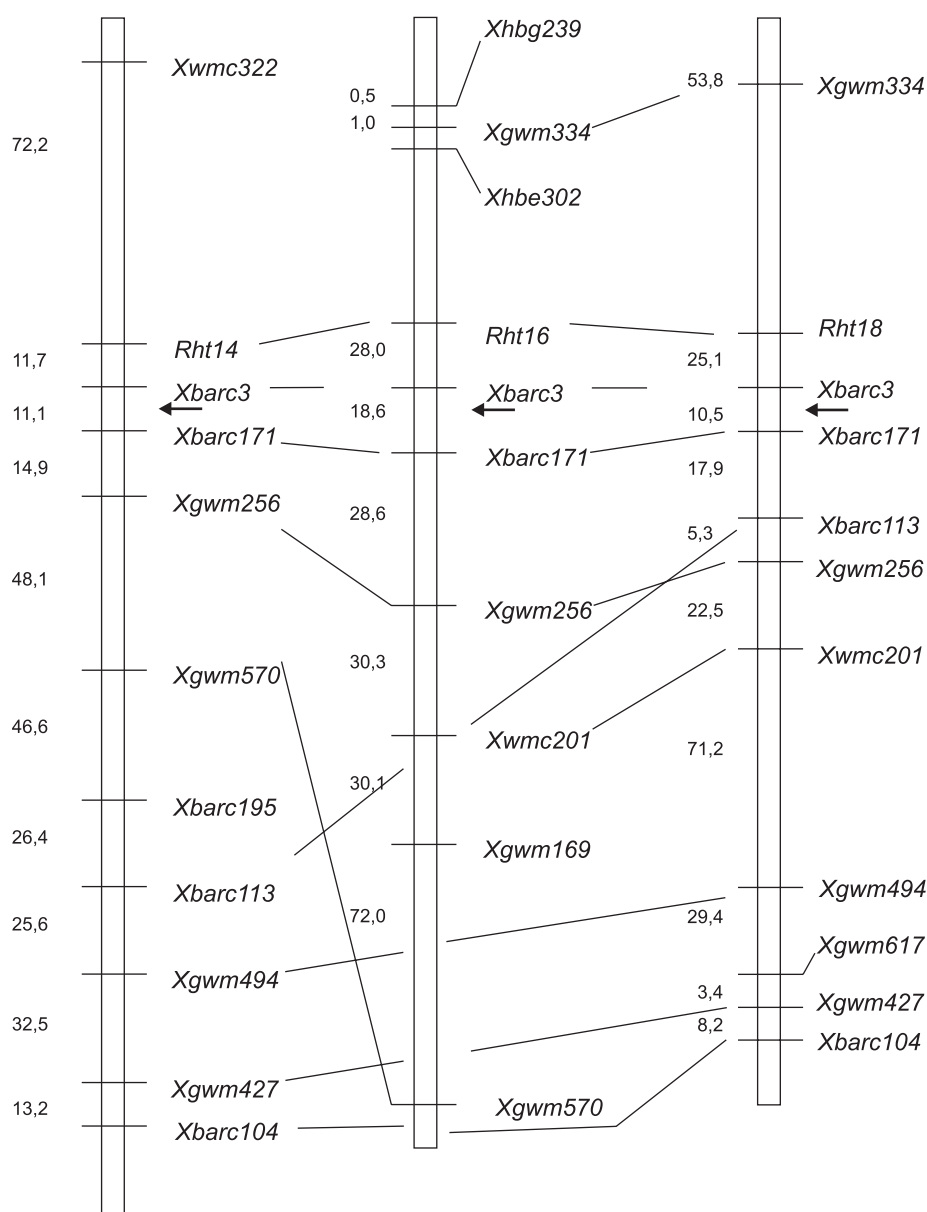


Figure 1. Linkage maps for *Rht14*, *Rht16* and *Rht18* genes on chromosome 6A. Arrows indicate the supposed position of centromere. Distances between the markers are shown in cM.

Xbarc3 on chromosome 6AS. Microsatellite mapping indicated that they were located at the same locus on the short arm of chromosome 6A (Fig. 1).

For homoeologous group 7 chromosomes, the genes (*P1* and *P2*) which determine elongated glumes were introduced from *T. polonicum* and

T. ispahanicum to LD222. Chlorina mutants were also determined by homoeologous genes on group 7 chromosomes (Klindworth *et al.*, 1995, Klindworth *et al.*, 1997). They were introduced to LD222. The genes for purple culm and chocolate black chaff on chromosome 7B were also introduced to LD222. Summarizing Table 1

and Table 2, the genes for 12 near-isogenic lines were transferred from hexaploid wheat. The donors of genes for 29 near-isogenic lines were from tetraploid wheat.

Discussion

The near-isogenic lines are not well utilized resources. They may be used to study variation in plant performance such as plant height, number of tillers, spike length and seed dormancy. The *Rht-B1b* allele encodes a mutant form of a DELLA protein, a gibberellic acid (GA) signalling repressor (Peng *et al.*, 1999). *Rht-B1b* allele is associated with a single base-pair change leading to a TAG stop codon. Variation among multiple alleles at *Rht-B1b* locus may suggest that there is nucleotide sequence polymorphism in the semi-dwarfing genes.

The author intended to use several different donors to develop near-isogenic lines. For the gene for long glume, this was successful because a tetraploid species *T. polonicum*, a hexaploid species *T. petropavlovskyi* and Portuguese landraces of *T. aestivum* have the long glume trait which is controlled by *P1* gene. The author has also found the homoeologous gene *P2* on chromosome 7B (Watanabe, 1999). As shown in Table 2, black glume and hairy glume traits were also derived from plural sources.

The genetic collection for the traits which were controlled by the genes on homoeologous chromosomes were for spherical grain, brittle rachis, red grain, long glume and chlorina. It must be said that they were scarce in tetraploid wheat. The effort to develop near-isogenic lines has been extended to introduce taxonomy-related traits such as spelt from *Triticum dicoccum*, tetraaristatus (awn on the glumes) from *Triticum carthlicum*, and the branched spike from *Triticum turgidum*.

References

- Börner A., Plaschke J., Korzun V., Worland A.J. Relationship between the dwarfing genes of wheat and rye // *Euphytica*. 1996. V. 89. P. 69–75.
- Dellaporta S.L., Wood J., Hicks J.B. A plant DNA miniprep: Version II // *Plant Mol. Biol. Rep.* 1983. V. 1. P. 19–21.
- Joppa L.R., Williams N.D. Langdon durum substitution lines and aneuploid analysis in tetraploid wheat // *Genome*. 1988. V. 30. P. 222–228.
- Joppa L.R., Cantrell R.G. Chromosomal location of genes for grain protein content of wild tetraploid wheat // *Crop Sci.* 1990. V. 30. P. 1059–1064.
- Joppa L.R. Chromosome engineering in tetraploid wheat // *Crop Sci.* 1993. V. 33. P. 908–913.
- Klindworth D.L., Williams N.D., Duysen M.E. Genetic analysis of *chlorina* mutants of durum wheat // *Crop Sci.* 1995. V. 35. P. 431–436.
- Klindworth D.L., Klindworth M.M., Williams N.D. Telosomic mapping of four genetic markers in durum wheat // *J. Hered.* 1997. V. 88. P. 229–232.
- Kosambi D.D. The estimation of map distances from recombination values // *Ann. Eugenics*. 1944. V. 12. P. 172–175.
- Kosuge K., Watanabe N., Kuboyama T. *et al.* Cytological and microsatellite mapping of mutant genes for spherical grain and compact spikes in durum wheat // *Euphytica*. 2008. V. 159. P. 289–296.
- Peng J., Richards D.E., Hartley N.M. *et al.* ‘Green Revolution’ genes encode mutant gibberellin response modulators // *Nature*. 1999. V. 400. P. 256–261.
- Qualset C.O., Soliman K.M., Jan C.-C. *et al.* Registration of UC66049 *Triticum aestivum* blue aleurone genetic stock // *Crop Sci.* 2005. V. 45. P. 432.
- Röder M.S., Korzun V., Wendehake K. *et al.* A microsatellite map of wheat // *Genetics*. 1998. V. 149. P. 2007–2023.
- Salina E., Börner A., Leonova I. *et al.* Microsatellite mapping of the induced sphaerococcoid mutation genes in *Triticum aestivum* // *Theor. Appl. Genet.* 2000. V. 100. P. 686–689.
- Schmidt J.W., Johnson V.A. A *sphaerococcum*-like tetraploid wheat // *Crop Sci.* 1963. V. 3. P. 98–99.
- Song Q.J., Shi J.R., Singh S. *et al.* Development and mapping of microsatellite (SSR) markers in wheat // *Theor. Appl. Genet.* 2005. V. 110. P. 550–560.
- Torada A., Koike M., Mochida K., Ogihara Y. SSR-based linkage map with new markers using an intraspecific population of common wheat // *Theor. Appl. Genet.* 2006. V. 112. P. 1042–1051.
- Watanabe N. Near-isogenic lines of durum wheat: their development and plant characteristics // *Euphytica*. 1994. V. 72. P. 143–147.
- Watanabe N. Genetic control of the long glume phenotype in tetraploid wheat by homoeologous chromosomes // *Euphytica*. 1999. V. 106. P. 39–43.
- Watanabe N. *Triticum polonicum* IC12196: a possible alternative source of GA3-insensitive semi-dwarfism // *Cereal Res. Commun.* 2004. V. 32. P. 429–434.
- Watanabe N., Fujii Y., Kato N. *et al.* Microsatellite mapping of the genes for brittle rachis on homoeologous group 3 chromosomes in tetraploid and hexaploid wheats // *J. Appl. Genet.* 2006. V. 47. P. 93–98.
- Watanabe N., Ikebata N. The effects of homoeologous group 3 chromosomes on grain colour dependent

- seed dormancy and brittle rachis in tetraploid wheat // *Euphytica*. 2000. V. 115. P. 215–220.
- Watanabe N., Imamura I. Genetic control of long glume phenotype in tetraploid wheat derived from *Triticum petropavlovskyi* Udacz. et Migusch. // *Euphytica*. 2002. V. 128. P. 211–217.
- Watanabe N., Nakayama A., Ban T. Cytological and microsatellite mapping of the gene for liguleless phenotype in durum wheat // *Euphytica*. 2004. V. 140. P. 163–170.
- Watanabe N., Sekiya T., Sugiyama K. *et al.* Telosomic mapping of the homoeologous genes for the long glume phenotype in tetraploid wheat // *Euphytica*. 2002a. V. 128. P. 129–134.
- Watanabe N., Sugiyama K., Yamagishi Y., Sakata Y. Comparative telosomic mapping of homoeologous genes for brittle rachis in tetraploid and hexaploid wheat // *Hereditas*. 2002b. V. 137. P. 180–185.
- Watanabe N., Takesada N., Fujii Y., Martinek P. Comparative mapping of the genes for brittle rachis in *Triticum* and *Aegilops* // *Czech. J. Genet. and Plant Breed.* 2005. V. 41. P. 39–44.
- Watanabe N., Yotani Y., Furuta Y. The inheritance and chromosomal location of a gene for long glume in durum wheat // *Euphytica*. 1996. V. 90. P. 235–239.
- Worland A.J., Sayers E.J. *Rht1* (*B. dw*), an alternative allelic variant for breeding semi-dwarf wheat varieties // *Plant Breeding*. 1995. V. 114. P. 397–400.