

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

Agronomy & Horticulture -- Faculty Publications

Agronomy and Horticulture Department

---

7-27-2005

## Quality effect of wheat-rye (1R) translocation in 'Pavon 76'

W. Kim

*Korea University, Anam-Dong, Seongbuk-Gu, Seoul 136-701, Korea*

J. W. Johnson

*University of Georgia, Griffin Campus, Griffin, GA*

P. Stephen Baenziger

*University of Nebraska-Lincoln, pbaenziger1@unl.edu*

A. J. Lukaszewski

*University of California, Davis, Riverside, CA*

C. S. Gaines

*USDA-ARS*

Follow this and additional works at: <https://digitalcommons.unl.edu/agronomyfacpub>



Part of the [Plant Sciences Commons](#)

---

Kim, W.; Johnson, J. W.; Baenziger, P. Stephen; Lukaszewski, A. J.; and Gaines, C. S., "Quality effect of wheat-rye (1R) translocation in 'Pavon 76'" (2005). *Agronomy & Horticulture -- Faculty Publications*. 116.  
<https://digitalcommons.unl.edu/agronomyfacpub/116>

This Article is brought to you for free and open access by the Agronomy and Horticulture Department at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Agronomy & Horticulture -- Faculty Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

## Quality effect of wheat-rye (1R) translocation in ‘Pavon 76’

W. KIM<sup>1</sup>, J. W. JOHNSON<sup>2</sup>, P. S. BAENZIGER<sup>3</sup>, A. J. LUKASZEWSKI<sup>4</sup> and C. S. GAINES<sup>5</sup>

<sup>1</sup>Division of Bioscience and Technology, College of Life and Environmental Sciences, Korea University, Anam-Dong, Seongbuk-Gu, Seoul 136-701, Korea, E-mail: kwook@korea.ac.kr; <sup>2</sup>Department of Crop and Soil Sciences, University of Georgia, Griffin Campus, Griffin, GA 30223; <sup>3</sup>Department of Agronomy and Horticulture, University of Nebraska, Lincoln, NE 68583; <sup>4</sup>Department of Botany and Plant Science, University of California, Davis, Riverside, CA 92521; <sup>5</sup>USDA-ARS Soft Wheat Quality Laboratory, Wooster, OH 44691, USA

With 3 tables

Received June 23, 2004/Accepted March 30, 2005

Communicated by W. E. Weber

### Abstract

A growing interest exists in using wheat for producing both hard and soft wheat products. It would be desirable if 1RS translocations in hard wheat could produce flour suitable for soft wheat products. The objective of this study was to test the effects of centric translocations of chromosome 1 from different rye sources for end-use quality. The quality influences of the 1RS and 1RL translocations and 1R substitutions from different rye sources were studied in a set of hard spring wheat ‘Pavon 76’ (CIMMYT) lines in three environments in Georgia. The protein concentration of the 1RL translocations was the highest while the 1RS translocations showed no difference in protein concentration compared with that of controls. The 1RS translocations increased alkaline water retention capacity while the 1RL translocations reduced it. T1DS-1RL was preferred for soft wheat products over other genotypes.

**Key words:** *Triticum aestivum* — *Secale cereale* — translocation — wheat quality

Various wheat (*Triticum aestivum* L.)-rye (*Secale cereale* L.) translocation lines have been developed to increase genetic variation in genomes. Most common translocations in wheat breeding have been involved with the short arm of rye (1RS) because of the presence of disease resistance genes (Mettin et al. 1973, Zeller and Hsam 1983) and 1RS translocations are considered to be advantageous for grain yield (Villareal et al. 1991, Carver and Rayburn 1994, Kim et al. 2004). In contrast to these favourable effects of 1RS translocations on agronomic performance, they have been considered as deleterious for bread baking quality (Dhaliwal and MacRitchie 1990, Dhaliwal et al. 1990, Pena et al. 1990, Fenn et al. 1994). Bread baking quality of wheat is mainly determined by protein quantity and quality (Payne et al. 1981). Hard wheat has been selected for bread baking with high protein concentration, strong gluten strength and high water absorption capacity. Wheat gluten has two main subunits; glutenin and gliadin. High molecular weight (HMW) (*Glu-1*) and low molecular weight (LMW) (*Glu-3*) glutenin subunits and gliadin (*Gli-1*) loci play a major role in determining dough strength (Gupta et al. 1994). Introduction of rye protein secalins on 1RS into a wheat genome and/or loss of gliadins and LMW glutenin subunits on the short arm of wheat chromosome 1 may be involved in a dough-processing issue, i.e. an increased salt-water soluble protein concentration and a reduced dough strength and stickiness caused by decreased gluten concentration (Lee et al. 1995). In comparison of 1RS translocation

genotypes, T1AL-1RS lines had fewer deleterious effect on bread making quality than T1BL-1RS lines, although no difference was observed for protein concentration (Graybosch et al. 1993). Gupta et al. (1994) analysed the effects of glutenin alleles based on maximum dough resistance and ranked the effects of *Glu-D1* and *Glu-B1* as greater than that of *Glu-A1*. Therefore, the effects of 1RS translocations and 1R substitutions on 1B and 1D may reduce the dough strength because of the missing *Glu-D1* and *Glu-B1*, respectively. Also, significant effects of environment and genetic background on quality have been reported (Peterson et al. 1992, Fenn et al. 1994, Johnson et al. 1999). Deleterious effects of 1RS were not consistent among 1RS translocation lines. Some T1BL-1RS sister lines derived from a CIMMYT nursery showed good bread making properties (Pena et al. 1990). Johnson et al. (1999) reported that variation of milling and baking quality could be affected by genetic background and environmental factors. However, the effects of rye chromosome 1 on soft wheat quality have not been reported and the presence of 1RS on hard wheat could be beneficial for soft wheat products.

The objectives of the current study were to examine the quality influence of 1RS and 1RL translocations and 1R substitutions from different rye chromatin sources. Thus, the feasibility of using hard wheat flour, carrying rye chromosomes, suitable for soft wheat products was determined.

### Materials and Methods

The study used a set of spring wheat ‘Pavon 76’ (CIMMYT) lines with various chromosome substitutions and translocations (Kim et al. 2004). Overall, this experiment consisted of six substitution lines of 1R, 12 1RS translocation lines, four 1RL translocation lines and 17 control lines including ‘Pavon 76’. All lines were grown in a randomized complete block design in Plains, GA for 2 years (1998 and 1999), and in Tifton, GA (1999). As a result of the severe wind damage in Tifton, GA (1998), only samples from the second year were included. Standard cultural practices were followed at each location. In each location, 0.1 kg/ha Tilt (propiconazole: 1-[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl methyl]-1H-1, 2,4-triazole) was applied to control powdery mildew caused by *Erysiphe graminis* DC. ex Marat f. sp. *tritici*, leaf rust caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici*, and glume blotch caused by *Stagonospora nodorum* Berk.

Grain samples (500 g) were analysed at the USDA-ARS Soft Wheat Quality Laboratory, Wooster, OH, for milling and baking quality, with duplicates. The grain was tempered to 15% moisture before milling. Approved methods 26–32 (AACC 2000) were used for

adjusted flour yield. Softness equivalent (SE) was tested according to Gaines et al. (2000). Protein concentration, alkaline water retention capacity (AWRC) and lactic acid retention capacity (LARC) were estimated using approved methods 46-10, 54-50 and 56-11 (AACC 2000). ANOVA was performed using PROC GLM from PC-SAS 6.12 (SAS Institute, 1996). Environments and replicates (blocks) were considered as random effects, and genotypes were considered as fixed. 1RS translocation lines within genotype were compared for flour yield, SE, flour protein, AWRC and LARC.

## Results

The primary object of this experiment was to determine the influence of the centric translocation of various rye chromatins (1RS and/or 1RL) and their sources on milling and baking parameters. Significant genotype (G)  $\times$  environment (E) interaction for flour yield, SE and flour protein (Table 1) may hinder precise evaluations of these traits. Significance of each comparison depends on environment because genetic background and environmental factors may affect milling and baking quality (Johnson et al. 1999). However, no serious changes on the mean rank of genotypes (data not shown) across the environments were observed.

Significant reduction of flour yield was observed in 1R substitutions and 1RL translocations compared with controls and 1RS translocations (Table 2). The effects of 1RS and 1RL translocations were significantly different for grain hardness and baking quality traits. This was probably a result of the combined effects of introducing a rye chromatin and replacing a wheat chromatin.

By comparing genotypes in each 1R substitution and 1RS translocation group, both 1RS translocations and 1R substitutions involved with wheat chromosome 1B had relatively higher SE than those of 1A and 1B (Table 3).

## Discussion

The measurement of milling properties is based on SE, and might not be indicative of grain hardness in this case. 1RS translocations had harder grain texture (e.g. lower SE values) on the contrary, 1RL translocations significantly increased SE

compared with 1R substitutions and controls. This result was consistent with the result of Graybosch et al. (1999) who reported significantly higher grain hardness of T1BL·1RS genotype compared with 1R(1B) substitution. They assumed that softer grains in 1R substitution could result from a gene or genes on 1RL that soften grains. They suggested rye HMW secalins might interfere with the protein–starch matrix and result in lower grain hardness. Given this hypothesis, flour extracted from 1RL translocations may include more free starch and finer flour after milling. On the contrary, 1RS translocation may increase damaged starch in flour fractions during milling, and these increases may affect the baking quality. Both 1R substitutions and 1RL translocations had significantly higher protein concentrations than controls and 1RS translocations. No effects of 1RL for protein concentration were reported by Graybosch et al. (1999). Higher protein concentration of 1RL translocations and 1R substitutions may be the result of the lower grain yield of these lines rather than the result of genes on 1RL. Both 1R substitutions and 1RL translocations from the field trial significantly reduced grain yields compared with 1RS translocations and controls (data not shown). No significant difference was observed in protein concentration between 1RS translocations and controls. Past studies indicated inconsistent results for the effects of 1RS on protein concentration. No effects of T1BL·1RS on protein concentration were reported (Dhaliwal et al. 1987, Graybosch et al. 1993), while reduced protein concentration of this translocation was reported (Fenn et al. 1994). Other studies reported higher protein concentrations in some 1RS translocations (Lee et al. 1995, Kim et al. 2003). AWRC, which is typically considered an indirect measure of pastry flour quality, was the lowest in the 1RL translocations although protein concentration was highest in 1RL translocations. Kim et al. (2003) indicated significant associations between AWRC and cookie diameter in T1DL·1RS compared with non-1RS lines in a population derived from a soft by hard wheat cross. The increased water absorption in 1RS translocations was at least partially dependent on the addition of rye secalin genes on 1RS. 1RS translocations had lower LARC than controls while 1RL translocations had higher LARC than the others.

Table 1: Mean squares for flour yield, SE, flour protein concentration at 12% moisture, AWRC and LARC of 6 1R substitutions, 12 1RS translocations, 4 1RL translocations and 17 controls in 'Pavon 76' grown in plains, GA in 1998 and 1999, and in Tifton, GA in 1999

Source	d.f.	Flour yield (%)	SE (%)	Protein (%)	AWRC (%)	LARC (%)
Environments (E)	2	18.7*	28.7*	136.0**	39.8**	1061.3
Blocks within E	1	0.1	0.1	1.8	21.8	5.0
Genotypes (G)	38	1.4**	25.7**	1.4**	9.7**	130.7*
G $\times$ E	76	0.2*	0.8*	0.3*	0.5	29.4
Error	114	0.1	0.5	0.2	0.4	30.4
CV (%)		0.4	2.4	3.7	1.0	7.0

SE, softness equivalent; AWRC, alkaline water retention capacity; LARC, lactic acid retention capacity. \*, \*\*Significant at  $P = 0.05$  and  $P = 0.01$ , respectively.

Table 2: Mean comparison of flour yield, SE, flour protein concentration at 12% moisture, AWRC and LARC of 6 1R substitutions, 12 1RS translocations, 4 1RL translocations and 17 controls in 'Pavon 76' grown in plains, GA in 1998 and 1999, and in Tifton, GA in 1999

Genotype	Flour yield (%)	SE (%)	Protein (%)	AWRC (%)	LARC (%)
All 1R substitutions (6) <sup>1</sup>	76.5 c <sup>2</sup>	29.3 b	12.2 b	62.6 b	79.2 c
All 1RS translocations (12)	77.3 a	26.6 c	11.6 c	64.4 a	79.0 c
All 1RL translocations (4)	76.8 b	33.1 a	12.5 a	60.6 c	90.6 a
All controls (17)	77.3 a	28.9 b	11.5 c	62.9 b	85.1 b
LSD ( $P = 0.05$ )	0.2	0.5	0.2	0.4	3.0

SE, softness equivalent; AWRC, alkaline water retention capacity; LARC, lactic acid retention capacity.

<sup>1</sup>Number of lines tested.

<sup>2</sup>Values with the same letter in the same column do not differ significantly at  $P = 0.05$ .

Genotype <sup>1</sup>	Flour yield (%)	SE (%)	Protein (%)	AWRC (%)	LARC (%)
<b>1R substitution</b>					
1R <sub>e</sub> (1A)	76.7 a <sup>2</sup>	28.5 c	12.2 ab	63.5 a	87.5 a
1R <sub>e</sub> (1B)	76.4 bc	30.6 a	12.1 b	62.5 b	77.8 bc
1R <sub>e</sub> (1D)	76.7 ab	28.4 c	12.1 b	61.6 c	73.8 c
1R <sub>rec</sub> (1A) (=1RS <sub>v</sub> ·1RL <sub>e</sub> )	76.4 bc	28.6 c	12.3 ab	63.8 a	84.7 ab
1R <sub>rec</sub> (1B) (=1RS <sub>v</sub> ·1RL <sub>e</sub> )	76.8 a	29.9 ab	11.8 b	62.3 b	73.7 c
1R <sub>rec</sub> (1D) (=1RS <sub>v</sub> ·1RL <sub>e</sub> )	76.3 c	29.6 b	12.8 a	62.8 bc	77.8 bc
LSD (P = 0.05)	0.3	0.9	0.6	0.7	8.7
<b>1RS translocation</b>					
T1AL·1RS <sub>am</sub>	77.9 ab	24.5 g	11.2 cd	66.0 a	83.2 ab
T1AL <sub>p</sub> ·1RS <sub>e</sub>	77.9 ab	25.6 ef	11.7 a–d	65.1 b	84.8 a
T1AL <sub>p</sub> ·1RS <sub>v</sub>	77.9 a	25.3 fg	11.8 a–c	65.0 b	83.3 ab
T1BL·1RS <sub>cim</sub>	77.0 d–f	27.2 b–d	11.3 cd	63.7 cd	74.8 c
T1BL·1RS <sub>gnr</sub>	76.8 fg	27.7 a–c	11.6 a–d	64.8 b	77.6 bc
T1BL <sub>p</sub> ·1RS <sub>v</sub>	76.5 g	28.0 ab	11.4 b–d	64.3 b–d	79.0 a–c
T1BL <sub>p</sub> ·1RS <sub>e</sub>	77.0 d–f	28.2 a	11.3 b–d	63.5 d	79.2 a–c
T1BL <sub>v</sub> ·1RS <sub>e</sub>	77.3 c–e	28.4 a	11.2 d	63.8 cd	75.4 c
T1DL·1RS <sub>bb</sub>	76.9 e–g	26.4 de	12.0 a	63.5 d	75.0 c
T1DL·1RS <sub>w</sub>	77.4 cd	25.4 f	11.9 ab	64.7 b	77.8 bc
T1DL <sub>p</sub> ·1RS <sub>e</sub>	77.3 cd	26.9 cd	11.9 ab	63.6 cd	81.3 a–c
T1DL <sub>p</sub> ·1RS <sub>v</sub>	77.6 bc	25.9 ef	11.6 a–d	64.4 bc	76.6 bc
LSD (P = 0.05)	0.4	0.9	0.6	0.9	6.8
<b>1RL translocation</b>					
T1AS <sub>p</sub> ·1RL <sub>e</sub>	75.5 c	34.7 a	12.5 a	61.6 a	94.8 a
T1BS <sub>p</sub> ·1RL <sub>e</sub>	77.1 ab	32.0 b	12.4 a	61.5 a	88.5 a
T1DS <sub>p</sub> ·1RL <sub>e</sub>	76.9 b	32.7 b	12.5 a	59.7 b	90.3 a
T1DS·1RL <sub>bb</sub>	77.5 a	32.9 b	12.5 a	59.7 b	88.8 a
LSD (P = 0.05)	0.4	1.2	0.6	0.8	9.5
<b>Control [range (%)]</b>					
Controls (17) <sup>3</sup>	77.1–77.6	27.9–30.2	11.2–12.0	62.3–63.7	78.5–92.3
'Pavon 76'	77.3	28.8	11.2	63.2	84.4
LSD (P = 0.05)	0.4	0.7	0.5	0.6	7.3

Table 3: Mean comparison of flour yield, SE, flour protein concentration at 12% moisture, AWRC and LARC of 6 1R substitutions, 12 1RS translocations, 4 1RL translocations and 17 controls in 'Pavon 76' grown in plains, GA in 1998 and 1999, and in Tifton, GA in 1999

SE, softness equivalent; AWRC, alkaline water retention capacity; LARC, lactic acid retention capacity.

<sup>1</sup>e, E12165(CIMMYT); rec, reconstructed chromosome; v, 'Veery'; am, 'Amigo'; cim, E12169(CIMMYT); gnr, 'Genaro'; bb, BH1146/Blanco' rye; w, 'Wheaton'; p, 'Pavon'.

<sup>2</sup>Values with the same letter in the same column do not differ significantly at P = 0.05.

<sup>3</sup>Number of lines tested.

When both 1RS and 1RL were present in 1R substitutions, they lowered LARC. Both 1RL and the short arm of wheat chromosome 1 may be responsible for higher LARC. Therefore, protein quality was significantly affected by introducing 1RS and/or 1RL chromatin.

From the comparison of three 1RS<sub>e</sub> and three 1RS<sub>v</sub> translocations, which can eliminate the effects of the variation of the 1RS source, T1BL·1RS genotypes from both 1RS sources had significantly higher SE than controls, T1AL·1RS and T1DL·1RS genotypes. Both 1RS translocations and 1R substitutions involving wheat chromosome 1A had relatively higher AWRC and LARC than those of T1BL·1RS and T1DL·1RS genotypes, while no difference was observed in protein concentration. Comparing six 1RS translocation lines derived from E12165 and 'Veery', T1AL·1RS genotype also had relatively higher AWRC and LARC compared with T1BL·1RS and T1DL·1RS genotypes. Graybosch et al. (1993) reported that T1AL·1RS lines had fewer deleterious effects on baking quality than T1BL·1RS lines, without a difference in protein concentration. Glutenin allele (*Glu-A1*) on wheat chromosome A1 had less effect on dough resistance than those on chromosomes B1 and D1 (Gupta et al. 1994). There was no significant background variation in these lines after introducing 1RS into 'Pavon 76' by seven backcrosses because the source of 1RS present in all three translocations in each set was identical. Therefore, the differences among the genotypes in each set can be attributed to the wheat glutenin allele on the short arm of wheat chromosome 1 replaced by 1RS, or to the

interactions of the remaining loci as well as the secale loci on 1RS. Single degrees of contrast within each 1RS translocation genotype indicated some differences based on 1RS source. Their allelic composition at the *Sec-1* locus is different. The variation of mean parameters of each 1RS translocation genotype is relatively lower than those of 1RS translocation genotypes carrying an identical 1RS from same source. This result indicates that the effect of the 1RS source on SE and baking quality is not, relatively, as high as the position effect of 1RS, but can still cause genetic variation for baking quality. Therefore, quality defects can be kept to a minimum by careful selection of rye source, and T1BL·1RS and T1DL·1RS genotypes are the better choices for soft wheat quality than T1AL·1RS.

## References

- American Association of Cereal Chemists (AACC), 2000: Approved Methods of the AACC, 10th edn. The Association, St Paul, MN.
- Carver, B. F., and A. L. Rayburn, 1994: Comparisons of related wheat stocks possessing 1B or 1RS.1BL chromosomes: agronomic performance. *Crop Sci.* **34**, 1505–1510.
- Dhaliwal, A. S., and F. MacRitchie, 1990: Contributions of protein fractions to dough handling properties of wheat-rye translocation cultivars. *J. Cereal Sci.* **12**, 113–122.
- Dhaliwal, A. S., D. J. Mares, and D. R. Marshall, 1987: Effect of 1B/1R chromosome translocation on milling and quality characteristics of bread wheats. *Cereal Chem.* **64**, 72–76.

- Dhaliwal, A. S., D. J. Mares, and D. R. Marshall, 1990: Measurement of dough surface stickiness associated with the 1B/1R chromosome translocation in bread wheats. *J. Cereal Sci.* **12**, 165—175.
- Fenn, D., O. M. Lukow, W. Bushuk, and R. M. Depauw, 1994: Milling and baking quality of 1BL/1RS translocation wheats. I. Effects of genotype and environment. *Cereal Chem.* **71**, 189—195.
- Gaines, C. S., P. L. Finney, and L. C. Andrews, 2000: Developing agreement between very short flow and longer flow test wheat mills. *Cereal Chem.* **77**, 187—192.
- Graybosch, R. A., C. J. Peterson, L. E. Hansen, D. Worrall, D. R. Shelton, and A. Lukaszewski, 1993: Comparative flour quality and protein characteristics of 1BL/1RS and 1AL/1RS wheat-rye translocation lines. *J. Cereal Sci.* **17**, 95—106.
- Graybosch, R. A., C. J. Peterson, and O. K. Chung, 1999: Quality effects of rye (*Secale cereale* L.) chromosome arm 1RL transferred to wheat (*Triticum aestivum* L.). *J. Cereal Sci.* **29**, 211—216.
- Gupta, R. B., J. G. Paul, G. B. Cornish, G. A. Palmer, F. Bekes, and A. J. Rathjen, 1994: Allelic variation at glutenin subunit and gliadin loci, *Glu-1*, *Glu-3* and *Gli-1* of common wheats. I. Its additive and interaction effects on dough properties. *J. Cereal Sci.* **19**, 9—17.
- Johnson, J. M., C. A. Griffey, and C. H. Harris, 1999: Comparative effects of 1BL/1RS translocation in relation to protein composition and milling and baking quality of soft red winter wheat. *Cereal Chem.* **76**, 467—472.
- Kim, W., J. W. Johnson, R. A. Graybosch, and C. S. Gaines, 2003: The effect of T1DL.1RS wheat-rye chromosomal translocation on agronomic performance and end-use quality of soft wheat. *Cereal Res. Comm.* **31**, 301—308.
- Kim, W., J. W. Johnson, P. S. Baenziger, A. J. Lukaszewski, and C. S. Gaines, 2004: Agronomic effect of wheat-rye translocation carrying rye chromatin (1R) from different sources. *Crop Sci.* **44**, 1254—1258.
- Lee, J. H., R. A. Graybosch, and C. J. Peterson, 1995: Quality and biochemical effects of a 1BL/1RS wheat-rye translocation in wheat. *Theor. Appl. Genet.* **90**, 105—112.
- Mettin, D., W. D. Bluthner, and G. Schlegel, 1973: Additional evidence on spontaneous 1B/1R wheat-rye substitutions and translocation. In: *Proceedings of the International Wheat Genetics Symposium*, 4th, 179. Missouri Agricultural Station, Columbia, MO, USA.
- Payne, P. I., K. G. Corfield, L. M. Holt, and J. A. Blackman, 1981: Correlations between the inheritance of certain high molecular weight subunits of glutenin and bread-making quality in progenies of six crosses of bread wheat. *J. Sci. Food Agric.* **32**, 51—60.
- Pena, R. J., A. Amaya, S. Rajaram, and A. Mujeeb-Kazi, 1990: Variation in quality characteristics associated with some spring 1B/1R translocation wheats. *J. Cereal Sci.* **12**, 105—112.
- Peterson, C. J., R. A. Graybosch, P. S. Baenziger, and A. W. Grombacher, 1992: Genotype and environment effects on quality characteristics of hard red winter wheat. *Crop Sci.* **32**, 98—103.
- Villareal, R. L., S. Rajaram, A. Mujeeb-Kazi, and E. del Toro, 1991: The effect of chromosome 1RS.1BL translocation on the yield potential of certain spring wheat (*Triticum turgidum* L.). *Plant Breeding* **106**, 77—81.
- Zeller, F. J., and S. L. K. Hsam, 1983: Broadening the genetic variability of cultivated wheat by utilizing rye chromatin. In: *Proceedings of the International Wheat Genetics Symposium*, 6th, 161—173. Kyoto University Press, Kyoto, Japan.