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The absence of the short arm of chromosome 7B produces inhibition of N mobilization and decreases grain protein concentration in wheat (*Triticum aestivum* L.) cv. Chinese Spring

Nora FATTA, Carla CAPUTO, Atilio J. BARNEIX*

IBYF, Faculty of Agronomy, University of Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina

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Abstract – The ditelosomic line CSDT7BL of wheat (*Triticum aestivum* L.) cv. Chinese Spring (CS), in which the short arm of chromosome 7B is missing, has been described as accumulating less protein in the grain than the normal line. In the present paper, we studied the protein accumulation and N mobilization in CSDT7BL and CS grown in the field under two N fertilization regimes, over two successive years in field-grown plants. The N treatments applied as urea were 0 or 300 kg N/ha in the first year, and 0 or 200 kg N/ha with 50% ear amputation in the second year. In both years, the ditelosomic line showed a lower protein concentration in the grain than CS only in the fertilized treatment, while no differences were observed without N fertilization. CSDT7BL had a higher N concentration in the straw at maturity under N fertilization, indicating inefficient N mobilization under high N supply. Ear excision increased grain protein concentration only in the normal line and not in the ditelosomic line. It is concluded that in the short arm of wheat chromosome 7B, there is genetic information which determines N remobilization at high N supplies.

nitrogen mobilization / grain protein / *Triticum aestivum* L. / ditelosomic line / Chinese Spring

Résumé – L'absence du bras court du chromosome 7B inhibe la mobilisation de l'azote et diminue la concentration en protéines dans le grain de blé (*Triticum aestivum* L.) cv. Chinese Spring. La lignée ditélosomique du cultivar Chinese Spring de blé CSDT7BL, où le bras court du chromosome 7B est absent, accumule moins de protéines dans le grain que la lignée normale. Nous avons comparé l'augmentation et l'accumulation de protéines dans le grain et la mobilisation de l'azote chez Chinese Spring et sa lignée ditélosomique CSD7BL dans des conditions de champ, avec deux niveaux de fertilisation azotée et pendant deux années. La deuxième année la moitié des épis ont été coupés transversalement. La teneur en protéines dans le grain est inférieure chez la lignée CSD7BL uniquement en conditions de

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* Correspondence and reprints
barneix@ifeva.edu.ar

haute teneur en azote. Quand les épis ont été coupés la concentration en protéines n'augmente que dans la lignée normale. En conséquence nous proposons que, sur le bras court du chromosome 7B, se trouve une information génétique nécessaire à une mobilisation efficace de l'azote quand la disponibilité en azote est élevée.

mobilisation de l'azote / protéine de grain / *Triticum aestivum* L. / lignée ditélosomique / Chinese Spring

1. Introduction

Grain protein concentration is a major determinant in wheat baking and nutritional quality [17]. Although knowledge about the genetic control of most of the individual proteins of the wheat grain and the regulation of their deposition has increased [13], the physiology and the genetic control of total grain protein concentration is still far from clear, due to important interactions between environmental conditions and the final grain protein concentration.

Most genes involved in the regulation of protein concentration are considered to have a non-significant effect, and are difficult to identify because of the masking effects of the environment. As a consequence, most of the wheat chromosomes and chromosome groups have been reported as affecting grain protein concentration [10]. Beniani and Busch [2] observed a bimodal or trimodal frequency distribution for protein content among progenies, indicating the existence of more than one important gene for nitrogen (N) concentration in wheat. A major gene for protein concentration has been ascribed to chromosome 5D [16], and in *T. turgidum* it has been suggested that chromosome 6B has one or more genes for high protein [5, 9], but no such gene for high protein content has been identified.

Ditelosomic lines, in which a whole chromosome arm is missing, have been useful in mapping genes, and they have also been used to study the effects of different chromosome arms on characters of wheat. The ditelosomic lines of wheat cv. Chinese Spring (CS) have been extensively used for genetic studies [10]. Although it has been reported that no ditelosomic line of cv. Chinese Spring accumulated more protein in the grain than the normal line [11], it has been shown that the ditelosomic line of Chinese Spring, CSDT7BL, in

which the short arm of chromosome 7B is missing, presents a lower grain protein concentration than the normal line, with little effect on grain yield [1]. This effect is unique to the CSDT7BL line, for all other 36 ditelosomic lines of CS tested did not produce a similar result [1], and it has been postulated that a gene(s) important for the determination of grain protein content may be located in that chromosome arm. There is also evidence that this putative gene may have an additive effect, for tetraploid lines of CS for chromosome 7B show a higher protein concentration than the normal line (Barneix and Suarez, unpublished).

In the present paper, we have studied the growth and N utilization by Chinese Spring wheat and by the ditelosomic line CSDT7BL grown in the field in order to characterize the process regulated by the genetic information located in chromosome 7B that may be responsible for affecting grain protein concentration.

2. Materials and methods

Seeds of Chinese Spring wheat and its ditelosomic line CSDT7BL were provided by the Cereal Research Department, John Innes Centre, U.K., and multiplied in the field. The experiments were carried out in the experimental field of the Faculty of Agronomy, University of Buenos Aires, Buenos Aires, Argentina, on a typical argiudol with an organic matter content of 2.5% and a total N content of 0.14%, which had previously been cultivated with maize for several years.

The experiments were performed over two successive years. The experimental design was a randomized block design with five blocks, and two levels of N fertility (0 kg N/ha, or 100 kg N/ha at sowing plus 100 kg N/ha at heading + 100 kg N/ha

at flowering applied as urea). In the second experiment (Expt. 2), the levels of N fertility were as follows: 0 kg N/ha or 100 kg N/ha at sowing plus 100 kg N/ha at heading, with no application at flowering. Seeds were sown in 1.0-m long plots, five rows/plot, at a density of 10 plants/m. In Expt. 2, in order to gather information on the effect of source/sink ratio on N remobilization in both lines, 95 days after sowing (DAS) (50% anthesis) in 50% of the fertilized or unfertilized plots all ears were transversally halved, and all the ears appearing in these plots after 50% anthesis were treated in the same way. At different times from anthesis to maturity plots were sampled, one linear m per plot (10 plants). Plants were separated into ears and straw, and dried at 60 °C for 48 h. At maturity grain and chaff were also separated. Total N concentration and grain protein concentration was determined through micro-Kjeldahl distillation after wet digestion in concentrated H₂SO₄ and H₂O₂.

3. Results

3.1. Experiment 1

When plants were grown in the field without fertilization or with 300 kg N/ha, plants of the normal line reached 50% anthesis 95 DAS, while plants of the ditelosomic line CSDT7BL showed

Table I. Accumulated biomass, fertile tillers and weight/ear at flowering in Expt. 1.

kg N/ha	Line	Biomass (g/plot)	Fertility (tillers/plot)	Ear weight (g/plot)
0	CS	98.1 (40)	72.3 (10.9)	29.0 (1.61)
	CSDT7BL	64.7 (25)	81.4 (9.77)	14.0 (1.25)
300	CS	228.6 (28)	107.0 (10.9)	34.0 (1.40)
	CSDT7BL	205.8 (28)	95.8 (10.9)	24.0 (1.40)
Significance				
	Line	NS	NS	***
	N	***	*	***
	Line × N	NS	NS	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error.

50% anthesis 98 DAS. At flowering no significant differences in biomass or ears/plot could be detected between lines, although there was a large response to N fertilization in both lines (Tab. I). However, the ears of CSDT7BL were smaller than those of the normal line (Tab. I) in both fertilizer treatments.

The N fertilization increased the N accumulated in the biomass and the ear N concentration, but no differences were observed between lines (Tab. II). At this time, there were no differences between lines or N treatments in straw N concentration or total N content per ear (Tab. II).

Table II. N accumulated in biomass, total N/ear, and straw and ear N concentration at flowering in Expt. 1.

kg N/ha	Line	Biomass total N (g/plot)	Total N/ear (mg)	Straw N concentration (% DM)	Ear N concentration (% DM)
0	CS	1.21 (0.34)	3.92 (0.47)	0.94 (0.06)	1.46 (0.068)
	CSDT7BL	0.70 (0.38)	4.10 (0.60)	1.05 (0.08)	1.24 (0.088)
300	CS	2.02 (0.48)	3.73 (0.74)	1.10 (0.10)	1.63 (0.108)
	CSDT7BL	2.28 (0.39)	4.26 (0.75)	1.17 (0.07)	1.48 (0.076)
Significance					
	Line	NS	NS	NS	NS
	N	**	NS	NS	*
	Line × N	NS	NS	NS	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error; DM: dry matter.

At maturity, an increase in biomass production in response to the fertilizer addition was observed, although no differences could be detected among lines (Tab. III). Despite the increase in grain yield produced by the fertilization, the plants of the CSDT7BL line yielded 30-40% less grain than the normal line, and produced smaller grains in both N treatments (Tab. III), but no differences in harvest index could be observed (Tab. III).

No significant differences in total plant N content were observed between genotypes (Tab. IV), although the fertilizer addition produced an

increase in both lines. The grain N content was also increased by the fertilizer addition, and the normal line accumulated more N in the grain than the ditelosomic line (Tab. IV). This line had a lower protein concentration in the grain than the normal line only in the fertilized treatment, with a significant interaction between line and fertilization (Tab. IV). The straw N concentration, on the other hand, was greater in the ditelosomic line in both N treatments (Tab. IV), and as a consequence, the N harvest index was lower in the CSDT7BL than in the normal line.

Table III. Accumulated biomass, grain yield, individual grains weight and harvest index at maturity in Expt. 1.

kg N/ha	Line	Biomass (g/plot)	Grain yield (g/plot)	Grain weight (mg/grain)	Harvest index
0	CS	99.5 (17.8)	19.0 (5.11)	25.3 (0.45)	29.5 (7.89)
	CSDT7BL	129.4 (15.4)	13.6 (5.11)	20.2 (0.39)	24.0 (6.83)
300	CS	225.8 (17.8)	42.2 (5.11)	25.9 (0.45)	23.3 (6.83)
	CSDT7BL	213.6 (17.8)	25.5 (5.11)	23.7 (0.45)	14.8 (7.89)
Significance					
	Line	NS	*	***	NS
	N	***	***	***	NS
	Line × N	NS	NS	*	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error.

Table IV. Grain protein concentration, total grain N, straw N concentration and N harvest index at maturity in Expt. 1.

kg N/ha	Line	Grain protein (% DM)	Total grain N (g/plot)	Total plant N (g/plot)	Straw N concentration (% DM)	N harvest index
0	CS	9.73 (0.47)	0.32 (0.17)	0.59 (0.19)	0.37 (0.034)	55.9 (9.86)
	CSDT7BL	9.56 (0.47)	0.23 (0.17)	0.82 (0.16)	0.49 (0.029)	41.8 (8.54)
300	CS	14.1 (0.47)	1.0 (0.14)	1.66 (0.16)	0.56 (0.029)	54.0 (8.54)
	CSDT7BL	11.2 (0.47)	0.49 (0.17)	1.62 (0.18)	0.66 (0.034)	29.8 (9.86)
Significance						
	Line	**	*	NS	**	*
	N	***	***	***	***	NS
	Line × N	*	NS	NS	NS	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error.

Table V. Accumulated biomass, fertile tillers, ears weight and straw weight at flowering in Expt. 2.

kg N/ha	Line	Biomass (g/plot)	Fertility (tillers/plot)	Ear weight (g/plot)	Straw weight (g/plot)
0	CS	62.4 (10.0)	25.9 (4.96)	5.25 (0.86)	56.1 (10.9)
	CSDT7BL	39.5 (10.0)	8.70 (4.96)	1.47 (0.86)	38.0 (9.79)
200	CS	84.4 (10.0)	30.7 (4.96)	6.55 (0.86)	77.0 (9.79)
	CSDT7BL	47.6 (10.0)	10.5 (4.96)	1.97 (0.86)	46.0 (9.79)
Significance					
	Line	***	***	***	***
	N	*	NS	NS	*
	Line × N	NS	NS	NS	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error.

3.2. Experiment 2

In the following year, both lines were compared in the same field, without fertilization or with 200 kg N/ha. At flowering, half the ear was excised in 50% of the plants in order to alter the source/sink ratio. At this time, N fertilization had increased the biomass in both lines (Tab. V), while line CSDT7BL had less biomass than the normal line, a smaller number of fertile tillers, and smaller ears. The total N content in the plants was higher in the normal line in both N treatments (Tab. VI),

Table VI. N concentration in the ear, N concentration in straw, and total N in biomass at flowering in Expt. 2.

kg N/ha	Line	Biomass total N (g/plot)	Straw N concentration (% DM)	Ear N concentration (% DM)
0	CS	0.57 (0.11)	0.92 (0.10)	0.94 (0.20)
	CSDT7BL	0.40 (0.11)	1.0 (0.10)	0.65 (0.20)
200	CS	1.07 (0.11)	1.37 (0.12)	1.87 (0.22)
	CSDT7BL	0.79 (0.11)	1.54 (0.12)	1.30 (0.28)
Significance				
	Line	***	NS	***
	N	***	***	***
	Line × N	NS	NS	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error.

with a higher N concentration in the ear of the normal line in both N treatments, with no differences in the straw N concentration.

At maturity, however, there were no differences were observed in biomass between lines, and although N fertilization increased yield in both lines, no differences were observed between lines or between intact or half-ear treatments. This compensation in the ear-excised plants was achieved through an increase in the individual grain weight and the number of ears in the ear-excised plants (Tab. VII). There was no effect of N fertilization on the individual grain weight or in the number of ears/plot, but the ditelosomic line had more ears than the normal line (Tab. VII).

The grain protein concentration showed a significant interaction between line and N fertilization, because the fertilizer addition increased the grain protein concentration only in the normal line, and not in the CSDT7BL line (Tab. VIII). Halving ear size increased the grain protein concentration, but there were significant interactions between line and the N fertilization treatment. In the normal line without fertilization, halving the ear increased the grain protein concentration by 18%, while no increase was observed in the ditelosomic line. Under N fertilization, on the other hand, ear halving again increased the grain protein concentration by 20%, while in the CSDT7BL line it increased the grain protein concentration by less than 10%

Table VII. Grain yield, accumulated biomass, ears/plot and individual grain weight at maturity in Expt. 2.

kg N/ha	Line	Ear treatment	Biomass (g/plot)	Grain yield (g/plot)	Grain weight (mg/grain)	Harvest index	Ears/plot
0	CS	Complete	279.5 (68.9)	64.5 (15.2)	27.2 (1.76)	24.0 (0.29)	127.0 (16.7)
		1/2	253.1 (68.9)	72.1 (15.2)	27.5 (1.76)	21.1 (0.29)	139.6 (18.7)
	CSDT7BL	Complete	217.1 (68.9)	54.1 (15.2)	21.6 (1.76)	26.1 (0.29)	175.0 (21.5)
		1/2	256.7 (68.9)	60.7 (15.2)	22.9 (1.76)	25.2 (0.29)	214.0 (21.5)
200	CS	Complete	487.6 (68.9)	75.6 (15.2)	25.5 (1.76)	15.8 (0.29)	128.0 (18.7)
		1/2	494.1 (68.9)	72.1 (15.2)	31.7 (1.76)	17.1 (0.29)	169.8 (18.7)
	CSDT7BL	Complete	426.3 (68.9)	100.3 (15.2)	24.0 (1.76)	24.1 (0.29)	174.7 (21.5)
		1/2	461.6 (68.9)	93.6 (15.2)	25.8 (1.76)	20.6 (0.29)	214.6 (16.7)
Significance							
	Line		NS	NS	***	*	***
	N		***	*	NS	*	NS
	Ear		NS	NS	*	NS	*
	Line × N		NS	NS	NS	NS	NS
	Line × ear		NS	NS	NS	NS	NS
	N × ear		NS	NS	NS	NS	NS
	Line × N × ear		NS	NS	NS	NS	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error.

Table VIII. Grain protein concentration, straw N concentration, N accumulated in biomass total grain N and harvest index at maturity in Expt. 2.

kg N/ha	Line	Ear treatment	Grain protein (% DM)	N harvest index	Total grain N (g/plot)	Total plant N (g/plot)	Straw N (% DM)
0	CS	Complete	11.1 (0.66)	68.1 (6.00)	1.26 (0.37)	1.47 (0.43)	0.26 (0.044)
		1/2	13.1 (0.66)	68.0 (6.00)	1.27 (0.37)	2.20 (0.43)	0.33 (0.044)
	CSDT7BL	Complete	12.0 (0.66)	66.0 (5.37)	1.08 (0.37)	1.64 (0.43)	0.34 (0.044)
		1/2	11.8 (0.66)	72.3 (6.00)	1.23 (0.37)	1.98 (0.43)	0.22 (0.05)
200	CS	Complete	12.9 (0.66)	53.5 (5.37)	1.78 (0.37)	3.66 (0.43)	0.30 (0.044)
		1/2	15.5 (0.66)	49.2 (6.00)	1.97 (0.37)	3.46 (0.43)	0.37 (0.05)
	CSDT7BL	Complete	11.3 (0.66)	45.8 (5.37)	1.95 (0.37)	3.50 (0.43)	0.52 (0.044)
		1/2	12.4 (0.66)	53.7 (5.37)	2.16 (0.37)	4.50 (0.43)	0.54 (0.044)
Significance							
	Line		***	NS	NS	NS	***
	N		*	***	***	***	***
	Ear		***	NS	NS	NS	NS
	Line × N		*	NS	NS	NS	**
	Line × ear		*	NS	NS	NS	*
	N × ear		NS	NS	NS	NS	NS
	Line × N × ear		NS	NS	NS	NS	NS

Asterisks indicate significant differences within each column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Figures in brackets represent the pooled mean standard error.

(Tab. VIII). The total N in grain was only increased by the N fertilization, without the effect of line or sink/source.

The N concentration in the straw at maturity was higher in the fertilized plots than in the unfertilized plots, and it was higher in the ditelosomic line than in the normal line in both N treatments, with a significant interaction between line and ear halving (Tab. VIII). No differences in harvest index could be detected between lines or ear excision, although there was a significant decrease due to the N fertilization (Tab. VIII).

4. Discussion

Although wheat is an allopolyploid, the absence of a chromosome arm deletes many genes that can account for some of the differences observed between CSDT7BL and the normal line, such as the longer cycle, the decrease in grain size or the decrease in yield.

In the present experiments the normal line presented a higher grain protein concentration than the ditelosomic line only in the fertilized plots, with no differences in the unfertilized treatment. These results contrast with previous results on experiments in soils of higher fertility, where protein concentration was found to be lower in the ditelosomic line with or without fertilization [1].

These results show that under high N supply the ditelosomic line transported a smaller proportion of the accumulated N to the ear than the normal line, causing a lower protein concentration in the grain in spite of the lower grain weight and yield, and a higher N concentration in the straw at maturity, while no differences in straw N concentration were detected during early grain filling. The lack of differences in protein concentration in the grain under a low N supply in both experiments indicates that the ditelosomic line can remobilize N as efficiently as the normal line when the N supply is low, but is less efficient when the N supply is high.

When the number of kernels allowed to develop on a spike is decreased, both the N content and

concentration of grains increase [7, 8, 12, 15], which could be explained as an increase of the photosynthates and amino acids available to the remaining grains. In Expt. 2, the plants with reduced grain number significantly increased the grain weight in both lines (Tab. VIII), but the increase in grain protein concentration presented significant interactions with genotype and fertilization. In the fertilized treatment, ear excision increased protein concentration only in the normal and not in the ditelosomic line, showing that although the N available to the remaining grains was increased, it was not transported to the ear.

The protein content in the grain depends upon the mobilization of N accumulated during vegetative growth, and the N accumulated after flowering. However, the way in which these two processes are regulated during grain filling is not completely clear. Field-grown wheat plants accumulate most of their N prior to anthesis [4], while during grain filling this N is mobilized from the vegetative organs to the grain. N mobilization depends on the activity of proteases that degrade proteins into amino acids, which are transported to the ear via the phloem [6]. The amino acids are exported to the phloem presumably through amino acid transporters [14], and the rate of export depends on the N availability to the plant, and the amino acid concentration in the leaf cell [3]. At this point, we cannot speculate about the physiological or biochemical cause of the deficient capacity to remobilize N under high N availability of line CSDT7BL, but the present results suggest that the short arm of wheat chromosome 7B provides important information for an efficient utilization of N fertilizers and production of grains of high protein content. The identification of this gene(s) may have important implications for breeding wheat of high baking quality/protein content. This line also represents an important tool for the study of the regulation of physiological and biochemical processes that determine the protein concentration in the grain.

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References

- [1] Barneix A.J., Fatta N., Kade M., Pflüger L., Suarez E.Y., The short arm of chromosome 7B affects grain protein concentration in wheat, *Cereal Res. Commun.* 26 (1998) 101–106.
- [2] Beniani N.F., Busch R.H., Grain protein inheritance and nitrogen uptake and redistribution in a spring wheat cross, *Crop Sci.* 32 (1992) 1471–1475.
- [3] Caputo C., Barneix A.J., Amino acids export to the phloem in relation to N supply in wheat (*Triticum aestivum* L.) plants, *Physiol. Plant* 101 (1997) 853–860.
- [4] Dalling M.J., The physiological basis of nitrogen redistribution during grain filling in cereals, in: Harper J.E., Schrader L.E., Howell R.W. (Eds.), *Exploitation of Physiological and Genetic Variability to Enhance Crop Productivity*, Am. Soc. Plant Physiol., New York, 1985, pp. 55–69.
- [5] Deckard E.L., Joppa L.R., Hareland G.A., Grain protein determination of the Langdon Durum-dicoccoides chromosome substitution lines, *Crop Sci.* 36 (1996) 1513–1516.
- [6] Feller U., Fisher A., Nitrogen metabolism in senescing leaves, *Crit. Rev. Plant Sci.* 13 (1994) 241–273.
- [7] Guitman M.R., Arnozis P.A., Barneix A.J., Effect of source-sink relations and nitrogen nutrition on senescence and N remobilization in the flag leaf of wheat, *Physiol. Plant* 82 (1991) 278–284.
- [8] Jenner C.F., Effects of shading or removing spikelets in winter wheat, testing assumptions, *Aust. J. Plant Physiol.* 7 (1980) 113–121.
- [9] Joppa L.R., Cantrell R.G., Chromosomal location of genes for grain protein content of wild tetraploid wheat, *Crop Sci.* 30 (1990) 1059–1064.
- [10] Konzak C.F., Genetic control of the content, amino acid composition, and processing properties of proteins in wheat, *Adv. Genet.* 19 (1977) 407–582.
- [11] Law C.N., Brown J.W.S., The co-operative program to grain protein differences among ditelocentric lines of the wheat variety Chinese Spring, IAEA-RC-66/1 (1977) 427–441.
- [12] Ma Y.Z., Mackown C.T., VanSanford D.A., Sink manipulation in wheat. Compensatory changes in kernel size, *Crop Sci.* 30 (1990) 1099–1105.
- [13] Müller M., Muth J.R., Gallusci P., Knudsen S., Maddaloni M., Motto M., Schmitz D., Sorensen M.B., Salamani F., von Wettstein D., Thompson R.D., Regulation of storage protein synthesis in cereal seeds; developmental and nutritional aspects, *J. Plant Physiol.* 145 (1995) 606–613.
- [14] Rentsch D., Frommer W.B., Molecular approaches towards an understanding of loading and unloading of assimilates in higher plants, *J. Exp. Bot.* 47 (1996) 1199–1204.
- [15] Simmons S.R., Moss D.L., Nitrate reductase as a factor affecting N assimilation during the grain filling period in spring wheat, *Crop Sci.* 18 (1978) 584–586.
- [16] Snape J.W., Hyne V., Altken K., Targeting genes in wheat using marker-mediated approaches, *Proc. 8th Int. Wheat Genetics Symp.*, Beijing, China, 1993, pp. 749–759.
- [17] Weegels P.L., Hamer R.J., Schofield J.D., Functional properties of wheat glutenin, *J. Cereal Sci.* 23 (1996) 1–18.