

Szent István University Gödöllő

# PRODUCTION, AGRONOMIC AND CYTOGENETIC ANALYSIS OF GENETIC STOCKS OF WHEAT

Main points of the thesis

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### 1. BACKGROUND AND AIMS OF THE RESEARCH

The whole history of human culture is reflected in a single grain of wheat, as in a mirror. We can see in it the woman who lived thousands of years ago and discovered that she benefitted if she sowed seed from plants whose spike axis was not fragile and which did not shed its seed. We can see the peasant farmer somewhere in Asia Minor who first selected hexaploid wheat because he realised that it could be used to make bread, and who should thus be respected as one of the greatest wheat breeders. We can see the enormous efforts made over thousands of years, which have resulted in the development of today's wheat varieties, which satisfy the contemporary requirements with respect to yield, quality and yield stability, i.e. they are resistant to various unfavourable environmental conditions such as frost, drought, high soil salt content and various diseases.

The breeding of new varieties, however, also leads to an increase in the vulnerability of the selected populations, since selection obviously shifts the population from the equilibrium state naturally developing in the course of evolution. This fact has encouraged scientists to include more and more genotypes in their breeding programmes and explains why such great financial and intellectual investments are made in the development and maintenance of gene banks. The gene pools of species related to cultivated wheat offer numerous unexploited opportunities for the improvement of various agronomic properties and for environmental protection. It is thus hardly surprising that such intense interest is now shown in these related species. Many research programmes are aimed at transferring genes, gene complexes or chromosomes from wild wheat species into cultivated wheat. In addition to practical considerations, crosses with wild species are also important from the theoretical point of view, since the degree of relationship can be deduced from the crossability, thus providing information on the evolutional process of hexaploid wheat. In this way the origin of two (A and D) of the three (ABD) genomes of hexaploid wheat has been clarified.

Among the abiotic environmental stress factors, drought is most frequently responsible for a reduction in the yield of agricultural crops, thus endangering the food sources of the human population. In addition to improvements in agrotechnical methods, improving the drought tolerance of crops, including wheat, is thus a major breeding aim. The achievement of this aim is not only desirable, but also feasible, since wheat and its relatives possess great genetic variability for this property. It is thus important to clarify the genetic regulation of drought tolerance, followed by the transfer of genes for this trait.

The translocation in which the short arm of the 1B chromosome of wheat was replaced through a central fusion by the short arm of the 1R rye chromosome had an enormous effect on wheat breeding worldwide. In wheat genotypes carrying the 1RS/1BL translocation, there is thus one pair of chromosomes which contains the short arm of the 1R rye chromosome and the long arm of the 1B wheat chromosome. According to the literature, almost four hundred wheat varieties now carry this translocation, but data on Hungarian varieties have only been available since the early nineties. It was thus thought desirable to carry out a new analysis on the whole of the Hungarian variety collection. Breeders are also endeavouring to obtain recombinations for the 1RS arm of the translocated chromosome, so it is important for them to know which varieties contain the translocation and in what genetic background.

The thesis summarises the results of three series of experiments:

The **first** was a crossing programme designed to create *Triticum aestivum/Aegilops cylindrica* addition lines. The fundamental aim of the classical crossing programme carried out with the wild tetraploid species, *Aegilops cylindrica* was to improve the frost resistance of *T. aestivum*. Various chromosome identification techniques were applied to analyse the chromosomes of the various lines. In the course of the experiment studies were made on the morphological and cytological properties and on certain quantitative traits of the hybrids.

The aim of the **second** series of experiments was to investigate the genetic control of drought tolerance. Chinese Spring/Agropyron elongatum and Chinese Spring/Imperial rye addition lines and Chinese Spring/Cappelle Desprez substitution lines were tested for drought tolerance in the Martonvásár phytotron to identify chromosomes and chromosome segments responsible for the development of this trait.

In the **third** series of experiments wheat varieties bred in the two major wheat breeding programmes in Hungary, at the Agricultural Research Institute of the Hungarian Academy of Sciences and in the Cereal Research Non-Profit Company, were tested for the presence of the 1RS/1BL translocation. If breeding is to be successful it is necessary not only to expand the gene pool and locate genes responsible for important agronomic traits, but also to carry out detailed genetic analyses on existing varieties.

It was also hoped to determine the frequency with which the 1RS/1BL translocation occurred in the Hungarian variety collection, since it is essential to obtain such knowledge on all potential breeding stocks if plant breeding is to become better targeted and better able to preserve the efficiency of valuable resistance genes over a longer period.

### 2. MATERIALS AND METHODS

MATERIALS USED IN THE EXPERIMENTS

Aegilops cylindrica  $\times$  Triticum aestivum hybrids were developed using four lines of the Aegilops cylindrica L. em. Thell. (2n=4x=CCDD) species, maintained in the Martonvásár Cereal Genebank and occurring wild in Hungary, and two varieties of *T. aestivum* L. em. Thell. (2n=6x=AABBDD), Chinese Spring (CS), which is widely used in wheat genetic experiments, and Martonvásári 14 (Mv 14), a variety which is still cultivated in Hungary.

For the genetic analysis of drought tolerance a Chinese Spring (CS)/Cappelle Desprez (CD) substitution series was used, with the exception of substitution lines 2A and 2B, which were not available, and vernalised plants of the recipient and donor varieties. Chinese Spring is moderately drought-tolerant, while Cappelle Desprez is drought-sensitive (Szabó-Nagy, 1992). The substitution series was developed by C. Law and his colleagues and was put at our disposal by J. Snape of the John Innes Institute, Norwich.

Disomic addition lines of CS/Agropyron elongatum, characterised by great drought tolerance, and CS/Imperial rye were examined. The CS/Agropyron elongatum addition series was developed by Dvořak and Knott (1974) and the CS/Imperial rye addition series by Driscoll and Sears (1971). Both were made available by the Wheat Genetic Resource Center, Manhattan, Kansas. Two wild species, Agropyron elongatum (2n=2x=14) and Agropyron intermedium (2n=2x=14), were also included in the experiments.

The occurrence of the 1RS/1BL translocation was tested on 66 bread wheat (*T. aestivum* L.) and 9 durum wheat (*T. durum* [Desf.] Husn.) varieties bred in the Cereal Research Institute (now Cereal Research Non-Profit Company) and in the Agricultural Research Institute of the Hungarian Academy of Sciences between 1978 and 1999 and included in the National Variety List published by the National Institute for Agricultural Quality Control in 1999.

The following bread wheat varieties bred by the Cereal Research Non-Profit Company were included in the investigations:

GK Tiszatáj, GK Csongor, GK Boglár, GK Ságvári, GK Kincső, GK Öthalom, GK Zombor, GK Szőke, GK Bence, GK István, GK Örzse, GK Bokros, GK Barna, GK Csűrös, GK Kata, GK Délibáb, GK Góbé, GK Olt, GK Zugoly, GK Pinka, GK Répce, GK Csörnöc, GK Marcal, GK Kende, GK Szindbád, GK Hattyas, GK Kalász, GK Élet, GK Malmos, GK Véka, GK Sára, GK Mérő, GK Cipó, GK Miska, GK Dávid, GK Kunság, GK Favorit, GK Garaboly, GK Mura, GK Forrás, GK Petur, GK Jászság, GK Verecke and GK Tenger.

The following bread wheat varieties bred by the Agricultural Research Institute of the Hungarian Academy of Sciences were chosen for the studies:

Mv 16, Mv 17, Mv 23, Fatima 2, Mv 25, Mv Optima, Mv Magma, Mv Emma, Mv Vilma, Mv Pálma, Mv Szigma, Mv Irma, Mv Magdaléna, Mv Matador, Mv Madrigál, Mv Mezőföld, Mv Martina, Mv Kucsma, Mv Summa, Mv Tamara, Mv Magvas and Mv Csárdás.

Of the 9 durum wheat varieties, GK Basa, GK Bétadur, GK Minaret, GK Novodur and GK Tiszadur originated from Szeged, while Martondur 1, Martondur 2, Odmadur 1 and Odmadur 2 were bred in Martonvásár.



The chromosome number was determined in the root tip and in pollen mother cells using the **Feulgen method**.

The chromosomes were identified using the **Giemsa C-banding method** (Friebe and Gill, 1994).

In experiments aimed at the **genetic analysis of drought tolerance** plants of the listed substitution and addition lines, together with the recipient and donor varieties were vernalised for the period required by the various genotypes (e.g. 42 days for Cappelle Desprez and the CS/CD 5A substitution, 21 days for Chinese Spring and other CS/CD substitution lines) and then planted in  $20 \times 20 \times 20$  cm pots containing 5 kg of a 3:1:1 mixture of garden soil, humus and sand, sterilised for 24 h at 82°C. Each pot contained three plants, which were raised in a PGB-96 chamber in the Martonvásár phytotron. The experiment was set up in a random block design with three replications. The plants were grown for 17 weeks under the conditions described in Table 3.1. The relative humidity was 64 % (day) and 76 % (night) throughout the experiment. The illumination was switched on and off in three steps, giving photosynthetic photon flux densities (PPFD) of 270, 320 and 350  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. The illumination intensity was 60, 70 and 74 J m<sup>-2</sup> s<sup>-1</sup>.

Weeks	Day temperature (°C)	Night temperature (°C)	Daylength (h)
1	14	10	13,5
2	15	11	14,0
3	16	12	15,0
4	16	13	15,0
5	17	13	15,5
6	17	14	15,5
7	18	14	16,0
8	18	14	16,0
9	18	14	16,0
10	18	14	16,0
11	18	15	16,0
12	19	16	16,0
13	20	17	16,0
14	21	18	16,0
15	22	19	16,0
16	23	20	15,5
17	24	20	15,5

Climatic programme used to raise plants of the CS/CD substitution series
in a PGB-96 phytotron chamber

The plants were divided into three irrigation groups:

E1: control, irrigated throughout the experiment

E2: drought stress in mid-season: irrigation was suspended from the beginning to the end of flowering, then continued up to full maturity

E3: drought stress during ripening: irrigation was suspended from the end of flowering, when seed filling began.

Parameters tested during the drought tolerance experiment:

The relative water content (RWC) was determined by cutting leaf sections of unit size from the flagleaf during drought stress in E2 and E3 and measuring the fresh mass (FW). The leaf sections were then dried in a drying cabinet for 24 h at 90°C to obtain the dry mass (DW). The relative water content was calculated from the data using the formula given by Ali Dib et al. (1990):

RWC (%) =  $[(FW-DW)/FW] \times 100$ 

To determine the relative water loss (RWL), six fully developed young leaves were sampled during the heading period. After measuring their mass they were wilted for 2 h at 30°C. After a further mass measurement they were dried at 100°C for 24 h to determine their dry weight. The extent of water loss was calculated using the equation given by Yang et al. (1991):

$$RWL = [(W_1 - W_2)/W_3]/[(t_1 - t_2)/60]$$

where  $W_1$ ,  $W_2$  and  $W_3$  are the initial, wilted and dry weights, and  $t_1$  and  $t_2$  the time when wilting began and ended in minutes.

The drought susceptibility index (DSI) was also calculated for each genotype using the equation given by Ali Dib et al. (1990):

$$DSI = (Y_i - Y_{ni})/Y_i$$

where  $Y_i$  was the grain yield of irrigated plants and  $Y_{ni}$  that of non-irrigated plants. **Data processing** 

The data were processed by bifactorial analysis of variance using the SPSS statistical program (Farshadfar et al., 1994).

In addition to Giemsa C-banding, genomic *in situ* hybridisation (Reader et al., 1994) and polyacrylamide gel electrophoresis (Jackson et al., 1996) were used for the identification of the 1RS/1BL chromosome translocation.

Zeiss (Opton), Zeiss Axioskop and Zeiss Ultraphot microscopes fitted with automatic or digital cameras were used for the cytological analyses and to prepare the photos, which had a magnification of  $1000\times$ .

### **3. RESULTS**

RESULTS ACHIEVED IN THE DEVELOPMENT OF *TRITICUM AESTIVUM* × *AEGILOPS CYLINDRICA* DISOMIC ADDITION LINES

Chromosome lines containing 44 chromosomes, selected from the self-pollinated  $BC_2$  progeny, were analysed by means of C-banding. Figure 1 shows the *Ae. cylindrica* chromosomes found in these lines in addition to the complete wheat chromosome set. The figure also shows two translocated wheat chromosomes. On the basis of C-banding it was thus possible to identify disomic addition lines carrying the  $2C^c$ ,  $E^c$  and  $F^c$  chromosomes.

The presence of dicentric and deletion chromosomes indicated that the *Ae. cylindrica* line used as crossing partner carried a gametocidic gene on the  $2C^c$  chromosome. This chromosome was present in most of the 44-chromosome lines. This fact confirms the presence of the gametocidic gene, since chromosomes carrying gametocidic genes are characterised by preferential transmission (Endo, 1988). For this reason, the *Ae. cylindrica* lines used in this crossing programme were not suitable for the development of a complete disomic addition series.



*Fig. 1. Ae. cylindrica* chromosomes  $(2C^c, E^c, F^c)$  demonstrated in the 44-chromosome lines by C-banding, together with translocation and deletion wheat chromosomes from the BC<sub>2</sub> generation

RESULTS OF THE GENETIC ANALYSIS OF DROUGHT TOLERANCE

Studies on the CS/CD substitution series led to the conclusion that drought tolerance is a complex polygenic trait and that the genes controlling stress adaptation are located on several chromosomes. Regions of outstanding importance were localised on the chromosomes of homoeologous groups 5 and 7.

The analysis of disomic addition lines of CS/A. *elongatum* and CS/Imperial rye confirmed the decisive role of these two homoeologous groups. The analyses also

supported the hypothesis that gene complexes promoting abiotic stress adaptation are to be found on chromosomes 5A, 5R and 5E (Sutka et al., 1995). These gene complexes contain favourable combinations of various alleles of the abiotic stress adaptation genes.

Snape et al. (1985) and Sutka and Snape (1989) located genes *Vrn1*, responsible for vernalisation, and *Fr1*, responsible for frost resistance, on wheat chromosome 5A. With the aid of RFLP markers Sutka et al. (1995) mapped these genes at a distance of 2.1 cM from each other. Galiba et al. (1992; 1993) confirmed that the 5A chromosome plays a role in the cold-induced accumulation of abscisic acid and in osmoregulation.

The existence of such complexes, consisting of combinations of closely linked genes, was hypothesised by Allard (1988), who based his theory on the examination of annual plants, chiefly barley.

Natural selection no doubt promotes the joint inheritance of such multilocus gene clusters, since they allow the plant to adapt more effectively to stress conditions.

# RESULTS OF EXPERIMENTS AIMED AT DETECTING THE 1RS/1BL TRANSLOCATION

### Analysis of the 1RS/1BL translocation using Giemsa C-banding

The 1RS/1BL translocation, which came about through a centric fusion, can be detected relatively easily by C-banding. Intensely stained intercalary and terminal bands are to be found on the long arm of wheat chromosome 1B, while there is a heterochromatic band complex near the centromere. The short arm of the 1B chromosome, which has a satellite, can be readily distinguished from the short arm of chromosome 1R, since numerous bands can be observed on the 1BS arm near the centromere and interstitially, while the short arm of chromosome 1R, which also has a satellite, has a very characteristic, strongly stained telomeric band and an equally characteristic subtelomeric band below the secondary restriction. A narrow heterochromatic band can be seen near the centromere (Fig. 2).



*Fig. 2.* Giemsa C-banding patterns of the 1B, 1R and 1RS/1BL chromosomes (the arrows mark the interstitial bands on the short arm of chromosome 1B, and the bands on the short arm, below the subtelomere and near the centromere on chromosome 1R)

In the course of Giemsa C-banding analysis, in addition to the 1RS/1BL translocation discussed here in detail, a further translocation (5BL/7BL; 5BS/7BS) was found in the variety GK Öthalom (Fig. 3).



Fig. 3. The 5BS/7BS-5BL/7BL reciprocal translocation

This translocation occurs, for example, in the variety Vilmorin 27 (Friebe and Gill, 1994) and, like the 1RS/1BL translocation, probably came about when the chromosomes fractured at the centromere in the univalent state during the metaphase of meiosis and then reunited in translocated form. The translocation no doubt represents a selection advantage under certain geographic and climatic conditions compared to varieties with normal 5B and 7B chromosomes. This could explain why the translocation is to be found, for example, in many French varieties.

Petróczi (2000) mentions the fact that GK Öthalom, which was registered in 1985, continues to give above-average yields in state variety trials. Its excellent adaptability has led to its being registered in Turkey, Romania and Yugoslavia. It would be interesting to carry out detailed C-banding analysis on the progeny of this variety, such as GK Miska, GK Élet and GK Petur, since this translocation could be of interest and value in improving the adaptability of new varieties. From this point of view, GK Petur could be particularly promising, since the other crossing partner in this case was a French variety, Thesee.

Further processing of the results of Giemsa C-banding analysis could continue to provide important information on the genetic background of Hungarian wheat varieties, e.g. on the extent of C-banding polymorphism to be found within the Hungarian varieties. Polymorphism may appear in the form of extra bands, in the absence of certain bands, or in differences in the sizes of the bands.

### Detection of the 1RS/1BL translocation using in situ hybridisation

*In situ* hybridisation was carried out using complete rye DNA on a number of varieties proved by SDS-PAGE and Giemsa C-banding to contain the 1RS/1BL translocation. One of the most promising new Martonvásár varieties, Mv Csárdás, was also included in this analysis (Fig. 4).



*Fig. 4.* Somatic chromosomes of Mv Csárdás in the metaphase of mitosis after genomic *in situ* hybridisation (GISH). As the result of GISH the rye chromosome arms fluoresce and show up light on the photo (the complete rye DNA was labelled with fluorogreen). The arrows mark the rye chromosome segments.

### Detection of the 1RS/1BL translocation using SDS-PAGE

SDS-PAGE analysis was carried out on the 66 Hungarian bread wheat varieties and 9 durum wheat varieties included in the experiment, all of which were state registered between 1978 and 1999. The control varieties were Avrora and Kavkaz, both known to carry the translocation, and Chinese Spring, which is known not to carry the translocation. An example of the results is presented in Figure 5.

On the basis of the results it can be seen that SDS-PAGE, Giemsa C-banding and genomic *in situ* hybridisation are all suitable for the detection of the 1RS/1BL wheat-rye translocation.

The results show that of the 66 Hungarian wheat varieties registered between 1978 and 1999 thirty-five, i.e. 53 % of the variety collection, contain the 1RS/1BL translocation, while this translocation could not be detected in any of the durum wheat varieties tested.

One danger which arises from time to time in various plant species is that a favourable gene or gene complex comes to be present in a large proportion of the breeding stock and in the cultivated varieties. A good example of this is the high frequency of the 1RS/1BL wheat-rye translocation in cultivated wheat varieties. This could be the source of considerable risk in the future.



Fig. 5. Storage protein patterns of wheat varieties. 1: Yubileinaya 50; 2: GK Tiszatáj; 3: GK Csongor; 4: GK Boglár; 5: GK Ságvári; 6: GK Kincső; 7: GK Öthalom; 8: GK Zombor; 9: Chinese Spring; 10: Kavkaz; 11: Avrora; 12: GK Szőke; 13: GK Bence; 14: GK István; 15: Mv 16; 16: Mv 17; 17: GK Örzse; 18: GK Bokros; 19: GK Barna. Varieties with or without the 1RS/1BL translocation can be distinguished on the basis of the  $\omega$ -gliadin band marked by the arrow. The gene for this protein is located on the short arm of chromosome 1B, so it is to be found in varieties with the normal 1B chromosome, but not in those with the 1RS/1BL translocation.

On the basis of pedigree databases, varieties carrying the 1B/1R translocation can be identified in the parental lines of the genotypes. If no such data are available on the parents, the presence of the translocation can be deduced by analysing their pedigrees for several generations.

The detection of the wheat/rye translocation in the selected varieties and lines was carried out by means of C-banding and genomic *in situ* hybridisation. Of the two methods C-banding is simpler and far cheaper and is also relatively fast. The analysis can be carried out within a week, including the time required for germination. The use of *in situ* hybridisation is justified if information is also required on the size of the translocation. The method is far more complicated and expensive than C-banding, but preliminary pedigree analysis can be carried out to avoid having to make this expensive test on genotypes certain to carry the translocation (all parents carry the translocation) or not to carry it (none of the parents carries it). A more precise knowledge of the genetic background of the breeding stock will contribute greatly to the creation of new populations with a broader genetic basis. One indication among the Martonvásár varieties registered in 2000. A variety of this type retains the storage protein genes on the short arm of chromosome 1B, which are more favourable for quality, while also carrying the resistance genes present on the short arm of the 1R chromosome.

### 4. NEW SCIENTIFIC RESULTS

**1.** The 2C<sup>c</sup>, E<sup>c</sup> and F<sup>c</sup> *Aegilops cylindrica* chromosomes were detected in wheat/*Aegilops cylindrica* disomic addition lines produced from crosses between *Ae. cylindrica* Host. × *Triticum aestivum* L. (Chinese Spring or Mv 14). In the course of the crossing programme plants containing translocated or deleted wheat chromosomes were identified. Sixteen of the 44-chromosome lines have been maintained up to the  $BC_2F_2$  generation.

**2.** The genetic control of drought tolerance in wheat was examined with the aid of a Chinese Spring/Cappelle Desprez substitution series and disomic addition series of Chinese Spring/*Agropyron elongatum* and Chinese Spring/Imperial rye. The analysis of the CS/CD substitution series led to the conclusion that drought tolerance is a complex polygenic trait and that the genes controlling stress adaptation are located on several chromosomes. It was found that most of the drought tolerance-related traits tested (relative water content, relative water loss, drought susceptibility index and grain yield) were controlled by genes on chromosomes 1A, 5A, 7A, 1B, 4B, 5B, 3D and 5D in wheat, 5E and 7E in *Agropyron* and 1R, 3R, 4R, 5R and 7R in rye. The regions with the significantly greatest effect were localised on chromosomes in the 5<sup>th</sup> and 7<sup>th</sup> homoeologous groups.

**3.** The 66 Hungarian bread wheat varieties and 9 durum wheat varieties registered between 1978 and 1999 were analysed by means of SDS-PAGE, Giemsa C-banding and genomic *in situ* hybridisation to discover whether they carried the 1RS/1BL wheat-rye translocation. Thirty-five (53 %) of the bread wheat varieties were found to carry this translocation, while it did not occur in any of the durum wheats tested. In the course of Giemsa C-banding a 5BS/7BS-5BL/7BL translocation was detected in GK Öthalom.

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