Theor Appl Genet (1989) 78:417–424

C-banding pattern and powdery mildew resistance of *Triticum ovatum* and four *T. aestivum – T. ovatum* chromosome addition lines

B. Friebe and M. Heun

Institute of Agronomy and Plant Breeding, D-8050 Freising-Weihenstephan, FRG

Received December 26, 1988; Accepted May 19, 1989
Communicated by K. Tsunewaki

Summary. C-banding patterns of *T. ovatum* (*Ae. ovata*) and four *T. aestivum* cv 'Poros'–*T. ovatum* chromosome addition lines are presented, and the added chromosomes of *T. ovatum* have been identified. Furthermore, nucleolar activity and powdery mildew resistance were analyzed in the 'Poros'-*ovatum* addition lines and compared to that of *T. ovatum* and *T. aestivum* cv 'Poros'. The addition lines II, III and IV and 'Poros' were highly susceptible to powdery mildew isolates nos. 8 and 9, whereas the addition lines VI_1 and VI_2 showed high resistance. Even for an Ml-k virulent isolate, these two lines were highly resistant. By combining the cytological results and those of the powdery mildew analysis, the added chromosomes of *T. ovatum* can be excluded from responsibility for the high powdery mildew resistance of the addition lines VI_1 and VI_2. The same is true for a modified chromosome *6B*, which is present in the 'Poros'-*ovatum* addition lines II, III and VI. The high variation in C-banding pattern observed in the A-, B- and D-genome complement of the addition lines is believed to be the result of crossing different lines of *T. aestivum* instead of 'Poros' alone. Thus, we cannot trace the powdery mildew resistance back to a specific chromosome.

Key words: Common wheat – *T. ovatum* – C-banding – Nucleolar activity – Powdery mildew resistance

Introduction

Many wild relatives of hexaploid wheat, *Triticum aestivum* (genomically AABBDD), are known to carry interesting genes, such as powdery mildew resistance (Gill et al. 1985), which might be useful in broadening the genetic variability of cultivated wheats. Due to the close evolutionary relationship of the genus *Aegilops*, which is now included in the genus *Triticum* (Bowden 1959), many of these wild *Triticum* species can be crossed quite easily with cultivated wheat. The obtained amphiploids and, later on, the derived chromosome addition lines are the first steps toward the incorporation of such new genes into cultivated backgrounds; exactly this is our intention in analyzing new possible sources for powdery mildew resistance.

This paper describes the C-banding pattern of the allotetraploid species *T. ovatum* (formerly *Aegilops ovata*, genomically UUMM, after Kimber and Sears 1987) and four *T. aestivum – T. ovatum* chromosome addition lines. In addition, the disease reaction of these lines against *Erysiphe graminis* f. sp. *tritici* is analyzed.

Materials and methods

The material analyzed consists of the hexaploid winter wheat cultivar 'Poros' (kindly provided by the gene bank of Braunschweig, FRG), *Triticum ovatum* (from Gatersleben, GDR) and the *T. aestivum* cv 'Poros'-*T. ovatum* addition lines II, III, IV and VI. These addition lines originated from D. Mettin, GDR, who attempted to increase the protein content by crossing *T. aestivum* with *T. ovatum* (Mettin et al. 1977).

Chromosome identification was carried out in 20–30 plants per line by phase contrast analysis and Giemsa C-banding, according to Giraldez et al. (1979). Nucleolar activity was analyzed by using the silver staining technique described by Lacadena et al. (1984). The methods used for testing powdery mildew resistance are described in detail by Heun and Fischbeck (1987a, b): leaf segments placed on agar containing 50 ppm bza were inoculated homogeneously and stored for 10 days at 17 °C ± 1 °C at low light intensity. Then, disease assessments were carried out by visual estimation of the infection grade (scale 0–9) and the infection type (scale 0–4). The pustule sizes were also recorded. These data were combined to form three classes: r = resistant, i = intermediate and s = susceptible. The powdery mildew isolates nos. 8 and 9 described by Heun and Fischbeck (1987b) and powdery mildew isolate no. 4a, possessing Ml-k virulence, were used.

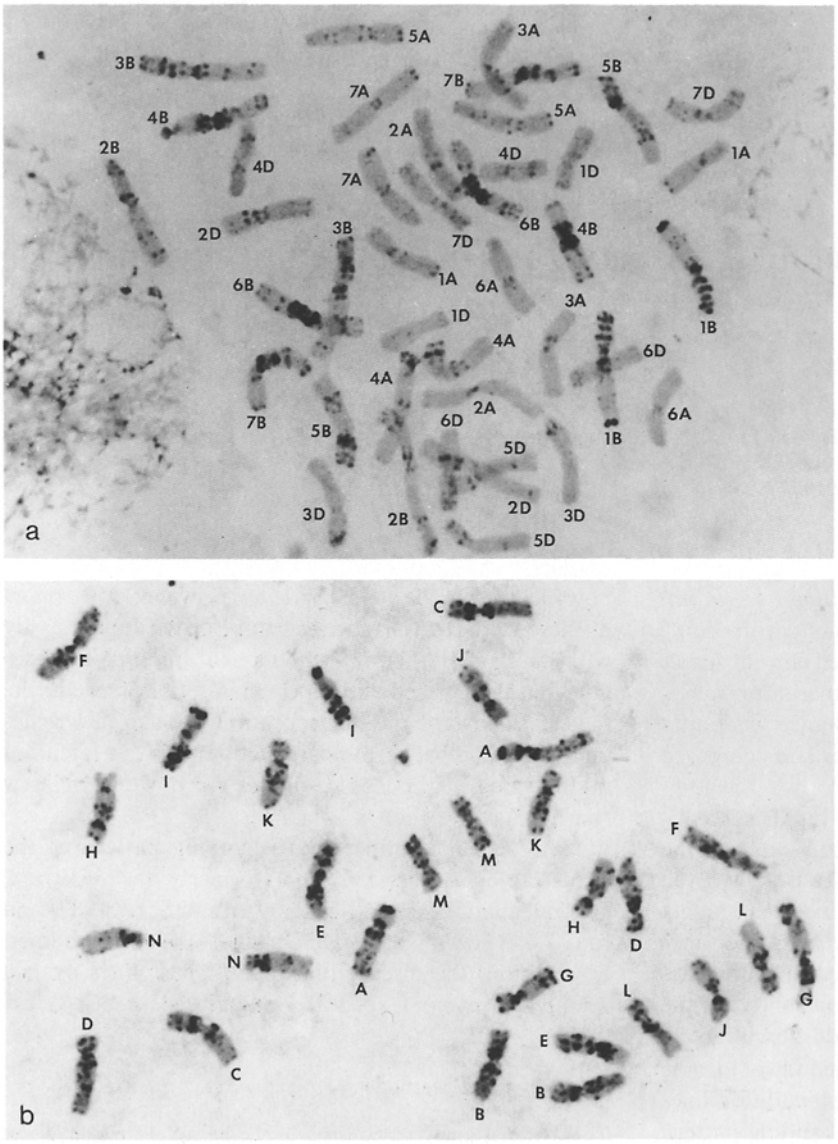

Fig. 1 a and b. C-banded mitotic metaphases of **a** *T. aestivum* cv 'Poros' and **b** *T. ovatum*

Results and discussion

C-banding pattern of T. ovatum

Figure 1 b shows C-banded mitotic metaphase of *T. ovatum*. A detailed karyogram of this line is given in Fig. 2. The arrangement of chromosomes according to size and arm ratios follows the study of Chennaveeraiah (1960). Since data on the relationship to the homoeologous groups of *Triticinae* do not yet exist, the chromosomes are lettered A to *N*.

Two chromosome pairs of *T. ovatum* show a secondary constriction in phase contrast, which were identified as chromosomes *A* and *I* after C-banding. Characteristic C-bands are also present in all the other chromosomes, allowing the identification of each chromosome pair. Only minor variation in C-banding pattern was observed within and between different plants of the *T. ovatum* line analyzed.

It is generally accepted that the U-genome of *T. ovatum* is closely related to that of the diploid ancestor *T. umbellulatum* (formerly *Aegilops umbellulata*), whereas the *M*-genome of *T. ovatum* corresponds to that of the diploid progenitor *T. comosum* (formerly *Aegilops comosa*) (Kihara 1937, 1946). Kimber and Sears (1983) proposed the genome symbols UU*MM* for *T. ovatum* to indicate that the *M*-genome of *T. ovatum* is modified compared with the M-genome present in *T. comosum*. By analyzing meiotic chromosome pairing in different hybrid combinations, Kimber et al. (1983) were able to show that the *M*-genome of *T. ovatum* has undergone

substantial structural rearrangements since its incorporation into *T. ovatum*, whereas the U-genome is much more closely related to that of the supposed ancestor *T. umbellulatum*. There is some evidence that the U-genome might also have been modified, however, to a much lesser degree than the *M*-genome (Kimber et al. 1987).

Teoh and Hutchinson (1983), Teoh et al. (1983 a) and Gill (1981) analyzed the C-banding pattern of diploid species belonging to the genus formerly named *Aegilops*. Whereas only minor variation in C-banding pattern was observed in *T. umbellulatum*, a large amount of intraspecific variation in C-banding pattern was observed in *T. comosum*. The polymorphic changes found n *T. comosum* include variation in C-band size and the presence or absence of bands within a basic pattern, as well as complete repatterning of the C-bands.

The presented karyotype of *T. ovatum* is almost completely different from that of the U- and M-genome of *T. umbellulatum* and *T. comosum*. An exception is the *N*-chromosome of *T. ovatum*, which corresponds to chromosome *F* of the C-banded karyotype of *T. umbellulatum* (Teoh and Hutchinson 1983). All the other chromosome pairs of *T. ovatum* show a C-banding pattern which differs from that of the diploid ancestors, indicating that both genomes have become modified since their incorporation into *T. ovatum*. This makes it impossible to identify which of the *T. ovatum* chromosome pairs belong to the U- and *M*-genome.

C-banding pattern of the A-, B- and D-genome chromosomes of 'Poros' and the 'Poros'-ovatum addition lines

Figure 1 a shows a C-banded mitotic metaphase of 'Poros'. The C-banding patterns of mitotic metaphases of the 'Poros'-*ovatum* addition lines are given in Fig. 3. A representative karyogram of 'Poros' and the 'Poros'-*ovatum* addition lines is shown in Fig. 4. (In accordance with the 7th International Wheat Genetics Symposium in Cambridge, 1988, chromosome *4A* and *4B* have been exchanged.)

All *A*-, *B*- and *D*-genome chromosome pairs of 'Poros' can easily be identified by their characteristic C-banding pattern. The C-banding pattern of 'Poros' is similar to that described for the hexaploid wheat cultivar 'Chinese Spring', which was established by analyzing aneuploid and telocentric lines (Lukaszewski and Gustafson 1983; Endo 1986; Gill 1987). However, it is well known that small differences in the C-banding pattern of individual chromosomes between different cultivars of wheat exist, which reflect the existence of polymorphisms of C-heterochromatin (Endo and Gill 1983, 1984; Friebe and Larter 1988).

In the present study, no differences in the C-banding pattern of individual chromosomes were observed within 'Poros' or any of the 'Poros'-*ovatum* addition lines: the smallest deviation between 'Poros' and the 'Poros'-*ovatum* addition lines arose in the addition line IV. The C-banding pattern of the wheat chromosomes in that line are nearly identical to that of 'Poros', with the exception of two faint interstitial C-bands in the long arm of chromosome *6A* and a subterminal band in the long arm of chromosome *7B*. Line IV is also the only addition line which carries a normal chromosome pair *6B*, whereas a modified *6B* was found in the addition lines II, III and VI.

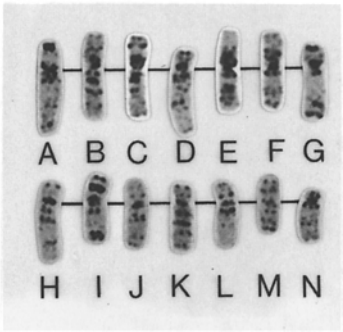

Fig. 2. C-banded karyogram of *T. ovatum*

In addition to the presence of a modified *6B*, differences in C-banding pattern of *2AS, 7AS, 7AL, 3BL* and *5BL* distinguish the wheat chromosome complement of the addition line III from that of 'Poros'.

Marker bands in *5AL, 2BL, 7BS, 2DS* and *2DL* show a similar deviation from the C-banding pattern of 'Poros' in the addition lines II and VI. Furthermore, both lines possess the same type of modified *6B*, which lacks the terminal C-band in the short arm, compared with the modified *6B* found in the addition line III. However, both lines differ in C-banding pattern from each other with respect to *1AL, 7AS, 7AL, 3BL, 7DS* and *7DL*.

The large amount of C-banding polymorphism found between the *A*-, *B*- and *D*-genome chromosomes of 'Poros' and those of the 'Poros'-*ovatum* addition lines was not expected since, as mentioned above, no polymorphism for C-heterochromatin was observed within the wheat cultivar 'Poros'. Structural rearrangements, which are known to occur during the production and further propagation of alien chromosome addition lines (Lukaszewski and Gustafson 1983; Friebe and Larter 1988), could not account alone for the high degree of variation observed. Thus, it seems probable that different parents were used in the production of these addition lines instead of pure 'Poros' crosses alone.

Identification of the added chromosome pairs of the 'Poros'-ovatum addition lines

The added chromosome pair in the 'Poros'-*ovatum* line II is sub-metacentric and shows a secondary constriction in

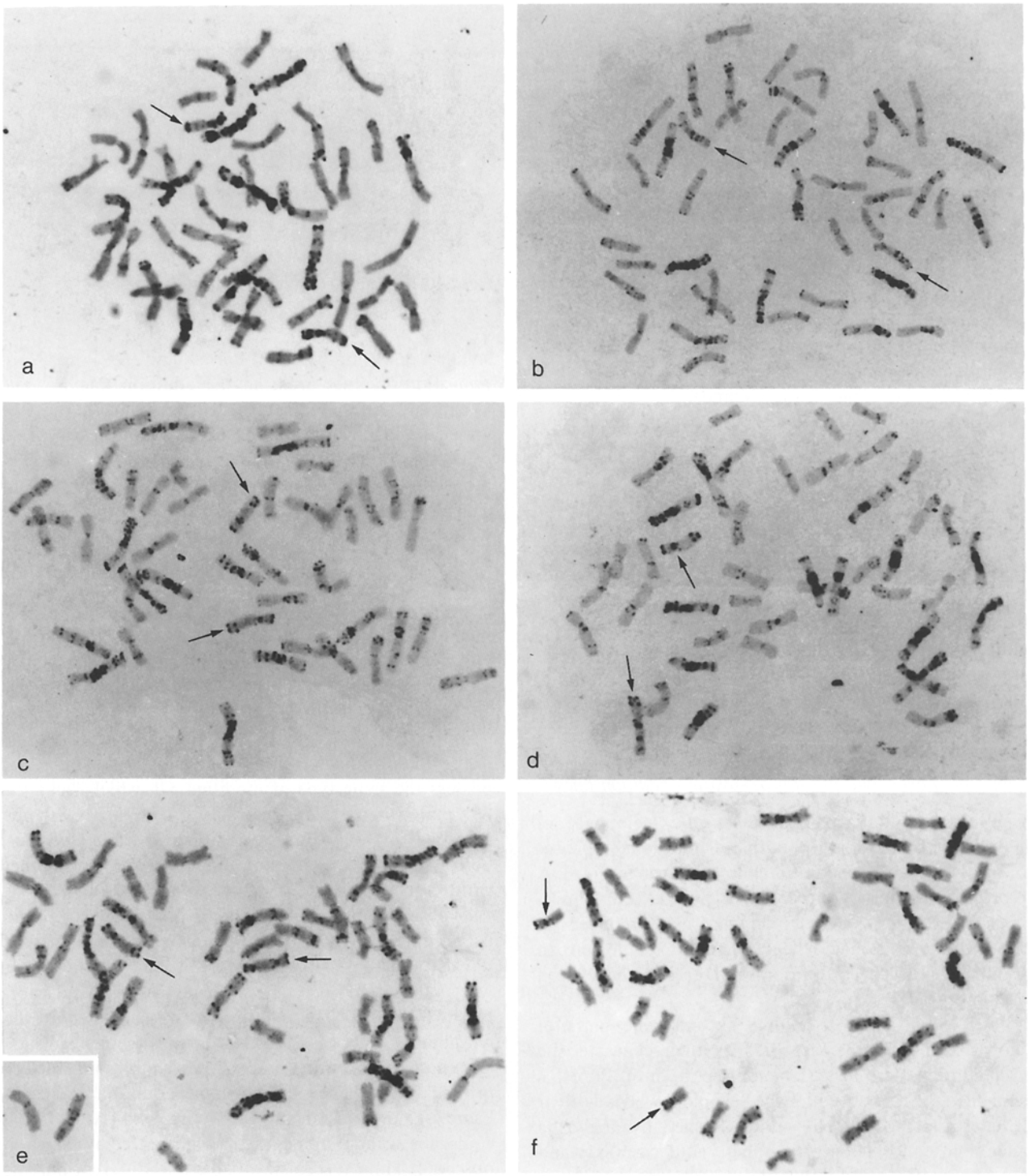

Fig. 3a–f. C-banded mitotic metaphases of the *T. aestivum* cv 'Poros-*T. ovatum* chromosome addition lines **a** II, **b** III, **c** IV homozygous, **d** IV heterozygous, **e** VI_1 and **f** VI_2 (added chromosomes of *T. ovatum* are marked with *arrows*)

the short arm in phase contrast. This arm is marked by a C-band adjacent to the centromere, a band located distally to the secondary constriction and a terminal C-band, whereas the long arm shows a pronounced terminal band and two faint bands – one located distally and one near the centromere. This chromosome is supposed to correspond to chromosome *I* of *T. ovatum*, which is very similar in its C-banding pattern, except that the proximal C-band in the long arm is more pronounced in chromosome pair *I* of *T. ovatum* than in chromosome *II*

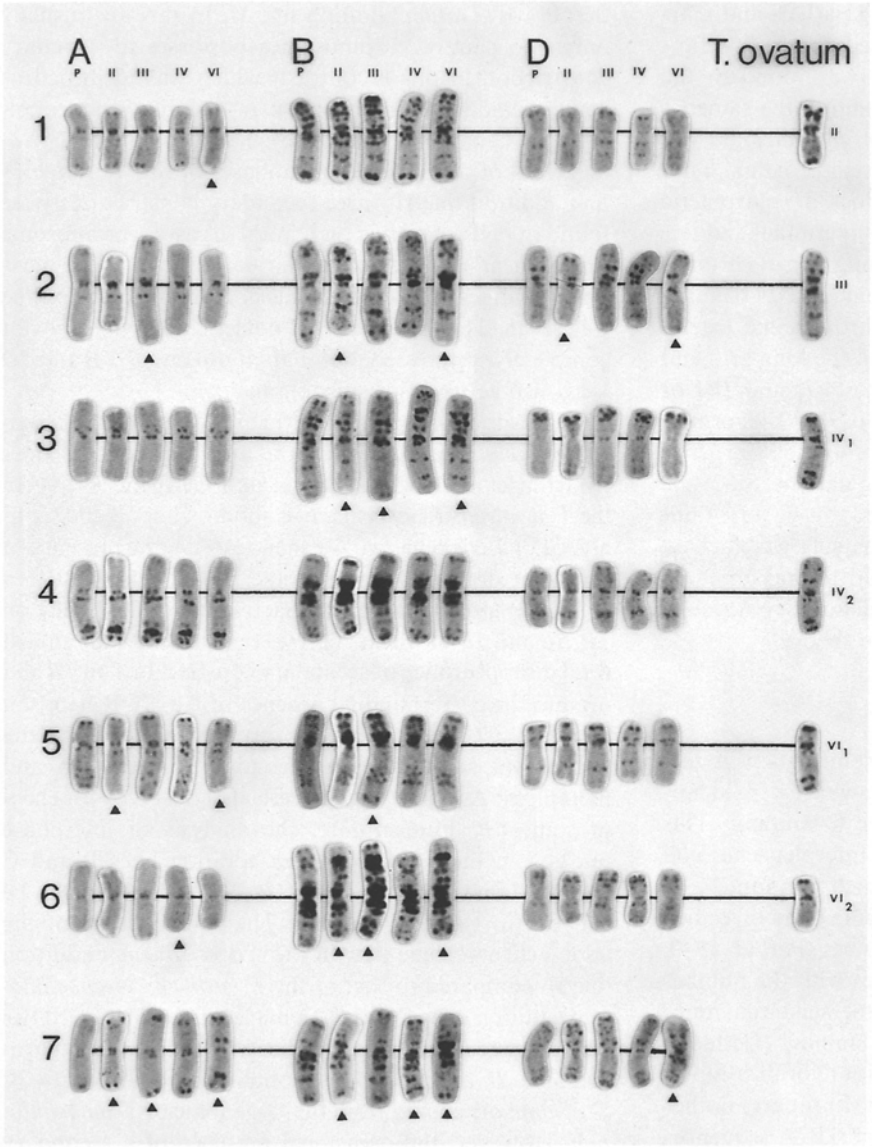

Fig. 4. C-banded karyogram of *T. aestivum* cv 'Poros' and the 'Poros'-*ovatum* chromosome addition lines (differences in C-banding pattern between 'Poros' and the *A*-, *B*- and *D*-genome chromosomes present in the addition lines are marked with *triangles*)

chromosome pair of *T. ovatum* is sub-metacentric and shows large C-bands on both sides of the centromere; a pronounced proximal, and faint subterminal and terminal bands in the short arm, and a proximal, interstitial and terminal band in the long arm. The corresponding chromosome of *T. ovatum* is chromosome *L*, which is similar in morphology and C-banding pattern but lacks the terminal band in the long arm.

Two different types of alien chromosomes were found in the 'Poros'-*ovatum* addition line IV, now designated as IV_1 and IV_2. Seventeen plants were homozygous for chromosome IV_1; eight were heterozygous for chromosomes IV_1 and IV_2. Chromosome IV_1 is sub-metacentric

ıal and small bands adjacent to the arms and a distinct subterminal C-ı. In addition, this chromosome possesses a large block of centromeric C-heterochromatin and another faint band in the long arm. The corresponding chromosome of *T. ovatum* is chromosome *G*, which additionally has another faint band in the distal region of the long arm.

The long arm of chromosome type IV_2 possesses the same C-banding pattern as the long arm of IV_1, whereas the short arm is marked by two interstitial C-bands which are characteristic for the long arm of chromosome *3B* of wheat.

Two different progenies of the 'Poros'-*ovatum* addition line VI were analyzed, called VI_1 and VI_2; the added chromosome pairs were designated VI_1 and VI_2. Chro-

mosome VI_1 is identical in C-banding pattern and morphology to chromosome IV_1 described above. A different type of alien chromosome pair was found in the progeny VI_2. The short arm of VI_2 shows the same C-banding pattern as the short arm of chromosome VI_1 and IV_1; it also contains the same small proximal band in the long arm and the same large block of centromeric C-heterochromatin, but it lacks the subterminal and terminal C-bands characteristic for the long arm of chromosomes VI_1 and IV_1. The morphology and C-banding pattern of VI_2 indicates that this chromosome carries either a deletion of the distal region in the long arm and is otherwise identical to chromosomes VI_1 and IV_1 or could be the result of a centric fusion of the short arm of chromosome VI_1 and the long arm of chromosome *6D* of wheat, which has a similar C-banding pattern. Since the centromeric region of *6D* is marked by a very faint C-band and chromosome VI_2 carries a large block of centromeric C-heterochromatin similar to that observed in chromosomes VI_1 and VI_1, the deletion hypothesis is more probable than the translocation theory.

Nucleolar activity

In *T. ovatum*, two pairs of chromosomes show a secondary constriction in phase contrast, which were identified as chromosomes *A* and *I* after C-banding. This agrees with the maximum number of interphase nucleoli observed after Ag-NOR banding, which was four.

The number of satellite chromosome pairs of *T. ovatum* corresponds to that in earlier reports (Pathak 1940; Chennaveeraiah 1960) and also agrees with the number of Ag-NOR bands at metaphase and the maximum number of nucleoli observed after silver staining (Cermeño et al. 1984a). However, by using in situ hybridization of a rRNA gene probe, Teoh et al. (1983b) found another pair of chromosomal sites which carry rDNA sequences in *T. ovatum*. Two pairs of chromosomes showing nucleolar activity were found in the supposed progenitors, *T. umbellulatum* and *T. comosum* (Cermeño et al. 1984a), whereas in *T. ovatum*, nucleolar activity of the *M*-genome was shown to be completely suppressed by the presence of U-genome originating from *T. umbellulatum*.

In hexaploid wheat two pairs of chromosomes, *1B* and *6B*, are known to show a secondary constriction. In addition, chromosome pair *5D* is also active in organizing nucleoli (Cermeño et al. 1984b). In 'Poros', as in other cultivars of hexaploid wheat, two pairs of chromosomes, *1B* and *6B*, have a secondary constriction in phase contrast. Furthermore, the maximum number of interphase nucleoli was six, indicating that three pairs of chromosomes, *1B*, *6B* and *5D*, were active in organizing nucleoli. A similar reaction was observed in the addition lines III and VI, which carry a modified *6B*. However, a partial inactivation of nucleolar activity was observed in the 'Poros'-*ovatum* addition line II. In this line, usually only one pair of chromosomes possesses a secondary constriction in phase contrast, which was identified as being the added chromosome pair – similar in morphology and C-banding pattern to chromosome I of *T. ovatum*. In 4 of 27 analyzed metaphases of the 'Poros'-*ovatum* addition line II, three secondary constrictions were found in phase contrast and, in these cases, chromosome *1B* of wheat also has a secondary constriction. The maximum number of interphase nucleoli observed in this line was seven. This indicates that nucleolar activity was not completely suppressed, but that NORs on *1B*, *6B* and *5D* were also active in organizing nucleoli.

This situation is similar to that reported for the *T. aestivum-T. umbellulatum* addition and substitution lines (Martini et al. 1982; Lacadena and Cermeño 1985). In the *T. aestivum-T. umbellulatum* addition lines B and C analyzed by Lacadena and Cermeño (1985), the presence of nucleolar organizer chromosomes *1U* and *5U* of *T. umbellulatum* produce a partial inactivation of the NORs on *1B*, *6B* and *5D* of wheat. This was expressed as the almost total disappearance of secondary constrictions on *1B* and *6B* and the corresponding absence of Ag-NOR bands at metaphase. However, this inactivation was not complete, because in some cases a secondary constriction and metaphase Ag-NOR bands were also observed on chromosome *6B*. Furthermore, the analysis of interphase nucleoli in the *T. umbellulatum* addition lines B and C indicates that chromosomes *1B*, *6B* and *5D* might be active in organizing nucleoli. The similar effect of the added chromosome pair in the 'Poros'-*ovatum* addition line II, compared to that of the *T. aestivum-T. umbellulatum* addition lines B and C on nucleolar activity of NORs belonging to wheat might indicate that the added chromosome *II* and the corresponding chromosome *I* of *T. ovatum* originated from the U-genome of *T. umbellulatum*. However, the occasional presence of a secondary constriction in *1B* observed in the 'Poros'-*ovatum* addition line II differs from the behavior of the *T. umbellulatum* addition lines. The different behavior of chromosome *6B* and the modified *6B* present in the 'Poros'-*ovatum* addition line II strengthens the modified character of this chromosome, whose origin is at present unknown.

Powdery mildew resistance

The above-mentioned genotypes (i.e. *T. ovatum*, *T. aestivum* cv 'Poros' and the 'Poros'-*ovatum* addition lines II, III, IV, VI_1 and VI_2) together with controls carrying known powerdy mildew resistance genes were inoculated with powdery mildew isolates nos. 8 and 9. Their reaction to different Pm/Ml-genes of the host is shown as follows:

Powdery mildew isolate no.	Virulent to the following Pm/Ml-genes									/	Avirulent		
8	1	2	3c	4a	4b	5**	*6**	8	9	/	3a	3b	k
9	2	3a	*3b**	3c	4a	4b	5	6	8	/	1	9	k

* The virulence of isolate no. 9 for *Pm 3b* and of isolate no. 8 for *Pm6* is incomplete, since intermediate host reactions occurred
** *Pm5* is assumed to be identical with Ml-i (Heun and Fischbeck 1987b)

T. ovatum and the 'Poros'-*ovatum* addition lines VI_1 and VI_2, which carry either a complete chromosome VI_1 or a deletion in the long arm of that chromosome, were highly resistant to the two powdery mildew isolates nos. 8 and 9, whereas 'Poros' and the 'Poros'-*ovatum* addition lines II, III and IV were highly susceptible. In spite of the fact the 'Poros'-*ovatum* addition line IV was, as described above, partly heterozygous for the added chromosomes IV_1 and IV_2, the disease reaction was homogeneously susceptible. The fact that both powdery mildew isolates are avirulent for Ml-k (a resistance gene originating from 'Kolibri', Heun and Fischbeck 1987b) led to an additional test of the resistant addition lines. After inoculation with powdery mildew isolate no. 4a, which possesses virulence for Ml-k, the 'Poros'-*ovatum* addition lines VI_1 and VI_2 were again highly resistant. Thus it can be concluded that these two lines are resistant to powdery mildew isolates carrying virulence for *Pm 1* to *Pm 9* and Ml-k. Therefore, these powdery mildew resistance genes are not responsible for the resistant reaction of the 'Poros'-*ovatum* addition lines VI_1 and VI_2. Since *Pm 3b* gave an intermediate reaction when inoculated with powdery mildew isolate No. 9, the only remaining possibility is that this resistance gene may be within the 'Poros'-*ovatum* addition lines VI_1 and VI_2, because it is possible – however, not probable – that the observed intermediate and high resistance to powdery mildew isolate No. 9 is the result of the same (*Pm 3b*) modified by different genetic backgrounds.

Combining the cytological characterization and the analysis of the powdery mildew resistance, it becomes evident that the added chromosomes of 'Poros'-*ovatum* lines VI_1 and VI_2 are not responsible for the good powdery mildew resistance. This can be concluded, because the 'Poros'-*ovatum* addition line IV also carries that chromosome, but is susceptible. Thus, the added chromosomes are definitely not the source of the observed powdery mildew resistance. Furthermore, the modified *6B* can be excluded, since this chromosome is also present in the 'Poros'-*ovatum* addition line II, which is susceptible. All other cytological differences among the lines were too variable to use them in searching for the source of powdery mildew resistance. This may be conditioned by the use of different wheat lines for producing the addition lines as shown above. By using 'Poros' alone, as we assumed at the beginning of these studies, it should have been possible to trace the powdery mildew resistance back to the underlying chromosomes; unfortunately, this cannot be done.

Acknowledgements. This work has been supported by a grant from the Deutsche Forschungsgemeinschaft.

References

Bowden WM (1959) The taxonomy and nomenclature of the wheats, barleys and ryes and their wild relatives. Can J Bot 37:130–136

Cermeño MC, Orellana J, Santos JL, Lacadena JR (1984a) Nucleolar activity and competition (amphiplasty) in the genus *Aegilops*. Heredity 53:603–611

Cermeño MC, Orellana J, Santos JL, Lacadena JR (1984b) Nucleolar organizer activity in wheat, rye and derivatives analyzed by a silver-staining procedure. Chromosoma 89:370–376

Chennaveeraiah MS (1960) Karyomorphologic and cytotaxonomic studies in *Aegilops*. Acta Horti Gotob 23:85–178

Endo TR (1986) Complete identification of common wheat chromosomes by means of the C-banding technique. Jpn J Genet 61:89–93

Endo TR, Gill BS (1983) Identification of wheat chromosomes by N-banding. In: Sakamoto S (ed) Proc 6th Intern Wheat Genet Symp Kyoto. Japan, pp 355–359

Endo TR, Gill BS (1984) Somatic karyotype, heterochromatin distribution, and nature of chromosome differentiation in common wheat, *Triticum aestivum* L. em Thell. Chromosoma 89:361–369

Friebe B, Larter EN (1988) Identification of a complete set of isogenic wheat/rye D-genome substitution lines by means of Giemsa C-banding. Theor Appl Genet 76:473–479

Gill BS (1981) Evolutionary relationships based on heterochromatin bands in six species of the *Triticinae*. J Hered 72:391–394

Gill BS (1987) Chromosome banding methods, standard chromosome band nomenclature and applications in cytogenetic analysis. In: Heyne EG (ed) Wheat and wheat improvement. American Society of Agronomy Monograph 13, Madison, pp 243–254

Gill BS, Sharma HC, Raupp WJ, Browder LE, Hatchett JH, Harvey TL, Moseman JG, Waines JG (1985) Evaluation of *Aegilops* species for resistance to wheat powdery mildew, wheat leaf rust, hessian fly and greenbug. Plant Dis 69:314–316

Giraldez R, Cermeno MC, Orellana J (1979) Comparison of C-banding pattern in the chromosomes of inbred lines and open pollinated varieties of rye, *Secale cereale* L. Z Pflanzenzuecht 83:40–48

Heun M, Fischbeck G (1987a) Identification of wheat powdery mildew resistance genes by analyzing host-pathogen interactions. Plant Breed 98:124–129

Heun M, Fischbeck G (1987b) Genes for powdery mildew resistance in cultivars of spring wheat. Plant Breed 99:282–288

Kihara K (1937) Genomanalyse bei *Triticum* und *Aegilops*. VII. Kurze Übersicht über die Ergebnisse der Jahre 1934–1936. Mem Coll Agric Kyoto Univ 41:1–61

Kihara K (1946) Genomanalyse bei *Triticum* and *Aegilops*. IX. Systematischer Aufbau der Gattung *Aegilops* auf genomanalytischer Grundlage. Cytologia 14:135–144

Kimber G, Sears ER (1983) Assignment of genome symbols in the *Triticinae*. In: Sakamoto S (ed) Proc 6th Intern Wheat Genet Symp Kyoto, Japan, pp 1195–1196

Kimber G, Sears ER (1987) Evoluation in the genus *Triticum* and the origin of cultivated wheat. In: Heyne EG (ed) Wheat and wheat improvement. American Society of Agronomy Monograph 13, Madison, pp 154–164

Kimer G, Pignone D, Sallee PJ (1983) The relationships of the M and M^u genomes of *Triticum*. Can J Genet Cytol 25:509–512

Kimber G, Sallee PF, Feiner MM (1987) The interspecific and evolutionary relationships of *Triticum ovatum*. Genome 30:218–221

Lacadena JR, Cermeño MC (1985) Nucleolus organizer competition in *Triticum aestivum-Aegilops umbellulata* chromosome addition lines. Theor Appl Genet 71:278–283

Lacadena JR, Cermeño MC, Orellana J, Santos JL (1984) Evidence for wheat-rye nucleolar competition (amphiplasty) in triticale by silver staining procedure. Theor Appl Genet 67:207–213

Lukaszewski AJ, Gustafson JP (1983) Translocations and modifications of chromosomes in triticale × wheat hybrids. Theor Appl Genet 64:239–248

Martini G, O'Dell M, Flavell RB (1982) Partial inactivation of wheat nucleolus organizers by the nucleolus organizer chromosomes from *Aegilops umbellulata*. Chromosoma 84:687–700

Mettin D, Blüthner WD, Schäfer HJ, Buchholz U, Rudolph A (1977) Untersuchungen an Samenproteinen in der Gattung *Aegilops*. Tagungsber Akad Landwirtschaftswiss DDR 158:95–106

Pathak GN (1940) Studies in the cytology of cereals. J Genet 39:437–467

Teoh SB, Hutchinson J (1983) Interspecific variation in C-banded chromosomes of diploid *Aegilops* species. Theor Appl Genet 65:31–40

Teoh SB, Hutchinson J, Miller TE (1983a) A comparison of the chromosomal distribution of cloned repetitive DNA sequences in different *Aegilops* species. Heredity 51:635–641

Teoh SB, Miller TE, Reader SM (1983b) Intraspecific variation in C-banded chromosomes of *Aegilops comosa* and *Aegilops speltoides*. Theor Appl Genet 65:343–348