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Cytological characterization, powdery mildew resistance and storage protein composition of tetraploid and hexaploid *1BL/1RS* wheat-rye translocation lines

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Summary. Progenies of a tetraploid *1BL/1RS* wheat-rye translocation line, CV 256, selected from the cross 'Cando' × 'Veery', were analyzed by means of Giemsa C-banding. CV 256 is cytologically stable for the presence of the *1BL/1RS* translocation but still segregating for *A*- and *B*-genome chromosomes of 'Cando' and 'Veery'. In CV 256, nucleolar activity of the *1RS NOR* locus is suppressed, as judged by the absence of a secondary constriction in that rye segment and the capability of organizing nucleoli. PAGE analysis of prolamins confirmed the presence of two 1RS secalins in all single seeds analyzed. SDS-PAGE analysis of reduced glutenins of single seeds indicated that some seeds contained the 'Cando' *Glu-B1* locus (subunits 6+8), some contained the 'Veery' *Glu-B1* locus (subunits 7+9) while others contained all four subunits, indicating that the material was heterozygous. *Pm8* resistance is expressed in the tetraploid *1BL/1RS* translocation line based on the reactions of six well-defined powdery mildew isolates. However, *Pm8* resistance is not expressed in the hexaploid wheat cultivars 'Olymp', 'Heinrich' and 'Florida', which also contain the *1BL/1RS* translocation. Obviously, the existence of the *1BL/1RS* translocation is not a proof for the expression of the associated genes. PAGE results did not show a clear linkage between powdery mildew resistance and the presence of 1RS secalins.

Key words: Wheat-rye translocations – Powdery mildew resistance – Gene expression – Storage proteins – C-banding

Introduction

Many Europaen cultivars of hexaploid wheat, *Triticum aestivum*, contain a segment of rye, *Secale cereale*, chromosome in the form of a translocation between the short arm of chromosome *1R* and the long arm of chromosome *1B* (Zeller and Fuchs 1983; Bennett 1984; Mettin and Blüthner 1984; Heun and Fischbeck 1978a). The short arm of rye chromosome *1R* is supposed to carry important genes for disease resistance against the wheat pathogens, *Puccinia striiformis* (yellow rust), *Puccinia recondita* (leaf rust), *Puccinia graminis* (stem rust) and *Erysiphe graminis* (powdery mildew). The resistance genes located on 1RS against these diseases are designated: *Yr9, Lr26, Sr31* and *Pm8* (McIntosh 1983).

Recently, the successful transfer of the *1BL/1RS* translocation from the hexaploid wheat cultivar, 'Veery', to the tetraploid durum cultivar, 'Cando', has been reported (Friebe et al. 1987). The present paper describes the cytological structure, composition of endosperm proteins and the reaction to the powdery mildew fungus of the tetraploid *1BL/1RS* translocation line, in comparison with some hexaploid *1BL/1RS* German winter wheat cultivars.

Materials and methods

The material analyzed consisted of the hexaploid spring wheat cultivar, 'Veery' (kindly supplied by A. Merker), which carries the *1BL/1RS* wheat-rye translocation of the Soviet winter wheat cultivar, 'Kavkas' (Merker 1982), the tetraploid North American durum cultivar, 'Cando' (kindly supplied by L. R. Joppa) and the self-pollinated offspring of a 28-chromosome line (designated CV 256) homozygous for the *1BL/1RS* translocation which was selected in the progeny of the cross 'Cando' × 'Veery' (Friebe et al. 1987). By crossing 'Cando' and 'Veery', five pentaploid F_1-plants were obtained, which were backcrossed to 'Cando', giving rise to 23 BC_1F_1-plants. Among the self-pollinated offspring of these BC_1F_1-plants, one plant (BC_1F_2) was selected which showed a chromosome number of 2n=28 and which was homozygous for the *1BL/1RS* translocation. Seed set of this plant was good and 63 BC_1F_3-plants were obtained which, together with 58 BC_1F_4-plants, were cytologically ana-

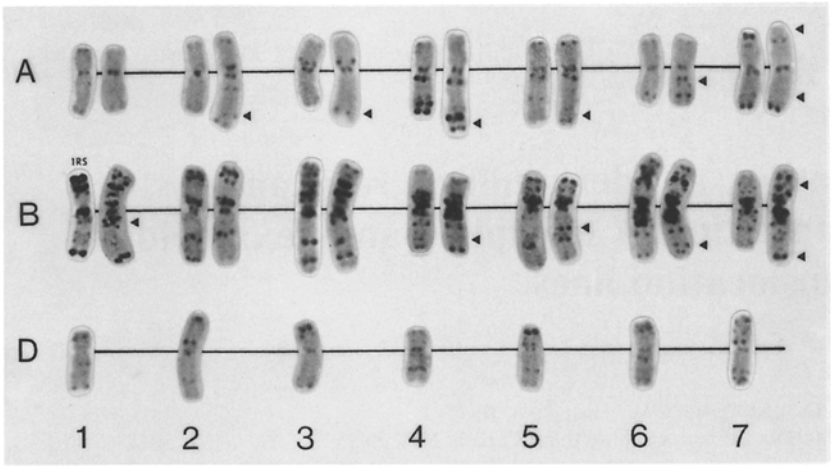


Fig. 1. C-banded karyograms of the hexaploid wheat cultivar, 'Veery' (left), and the tetraploid cultivar, 'Cando' (right). (Major differences are marked with *triangles*)

lyzed in the present study. The analysis of endosperm proteins was carried out on BC_1F_4-seeds and the disease resistance against powdery mildew was analyzed on BC_1F_5-plants.

Chromosome identification was carried out according to the Giemsa C-banding technique described by Giraldez et al. (1979). Nucleolar activity was analyzed by using Ag-NOR banding described by Lacadena et al. (1984). The composition of storage proteins was analyzed by polyacrylamide gel electrophoresis (PAGE) without and with sodium dodecyl sulfate (SDS-PAGE), according to Sapirstein and Bushuk (1985) and Ng and Bushuk (1987), respectively.

In addition to 'Veery', 'Cando' and CV 256, 17 cultivars/near-isogenic lines with known powdery mildew resistance genes (McIntosh 1983; Bennett 1984; Heun and Fischbeck 1987a) were used. Seeds of the near-isogenic lines were provided by J. G. Moseman; seeds of the cultivars were provided by the respective plant breeders (the German cultivars were obtained via the 'Bundessortenamt', Hannover, FRG). The virulences of the six powdery mildew isolates nos. 2, 5, 6, 85063, 85135 and W72/27 are described by Heun and Fischbeck (1987a, b); all these isolates are maintained and have been tested for more than three years.

The methods used for inoculation and disease assessment have been described previously (Heun and Fischbeck 1987a, b). Three 3-cm-long leaf segments taken from 10-day-old plants were placed on agar containing 50 ppm bza, and inoculated with approximately 300 spores/cm^2, using an improved settling tower. Ten days after inoculation, the visual disease symptoms were recorded, by assessing the infection type and the infection grade combined with notes about the pustule size. On the basis of these data, three major classes were formed: resistant (r), intermediate (i) and susceptible (s) host reaction. In some cases, however, this classification was unsatisfactory because of the variation observed and, therefore, a combined classification was introduced: e.g. r, i indicates that although mainly resistant reactions occurred, intermediate reactions were also observed. Three inoculation experiments were performed with each of the six powdery mildew isolates.

Results and discussion

Cytological characterization

Figure 1 shows C-banded karyograms of the hexaploid wheat cultivar, 'Veery' (left), and the tetraploid wheat cultivar, 'Cando' (right). (In accordance with the 7th International Wheat Genetics Symposium in Cambridge, 1988, chromosomes *4A* and *4B* have been exchanged.) All *A*-, *B*- and *D*-genome chromosomes can be identified easily by their characteristic C-banding, patterns which are similar to those described for other cultivars of wheat (Lukaszewski and Gustafson 1983; Endo 1986; Gill 1987; Friebe and Larter 1988). However, there are some cultivar-specific differences in C-banding patterns present between different cultivars of wheat, indicating the existence of polymorphism for C-heterochromatin in these genotypes (Iordanski et al. 1978; Endo and Gill 1983, 1984).

In the present study, 13 major differences in C-banding patterns between the *A*- and *B*-genome chromosomes of 'Cando' and 'Veery' were observed (Fig. 1). These marker bands are highly characteristic for these cultivars and can be used to follow the distribution of specific chromosome segments in segregating generations. It was possible to analyze the distribution of the 13 marker bands which differentiates 'Cando' from 'Veery' in 58 BC_1F_4-plants. Figure 2 shows a mitotic metaphase of one BC_1F_4-plant in phase contrast (a) and after C-banding (b). This plant was homozygous for the 'Cando'-type marker bands of the chromosome arms *2AL, 5AL, 7AS, 7AL, 1BL, 5BL* and *7BS*, homozygous for the 'Veery'-type marker bands *6AL, 4BL* and *6BL* and heterozygous for the marker bands in *3AL, 4AL* and *7BL*. A similar mixture of 'Cando'- and 'Veery'-type marker bands was also observed in the other progenies analyzed, indicating that this material is highly heterozygous and segregating for the *A*- and *B*-genome chromosomes of 'Cando' and 'Veery'.

The *1BL/1RS* translocation was easily identified according to large terminal and subterminal C-bands, which are characteristic for the short arm of rye chromosome *1R*. Altogether, 121 BC_1F_3- and BC_1F_4-plants of the *1BL/1RS* translocation line were analyzed, and in all

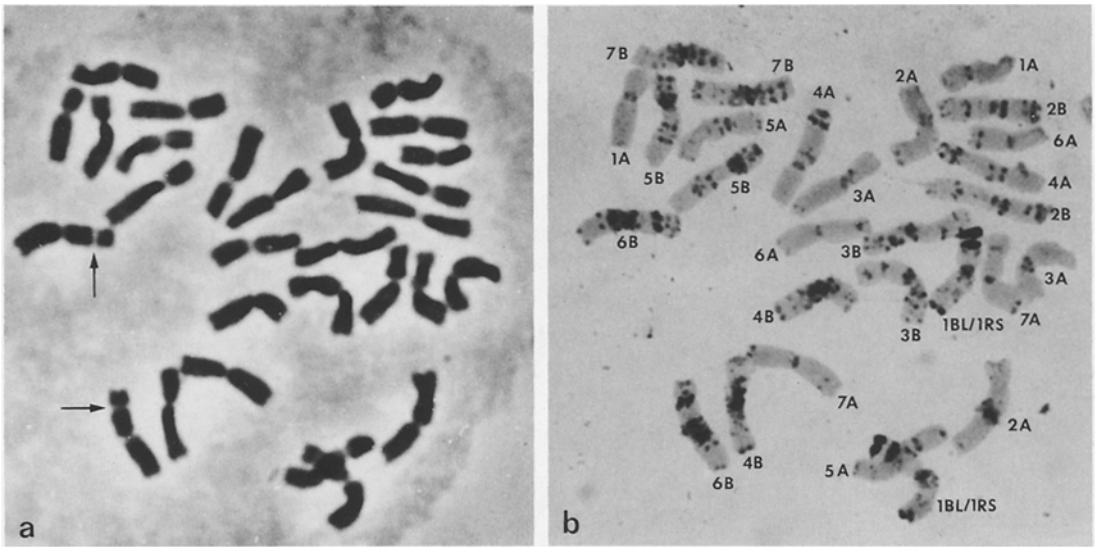
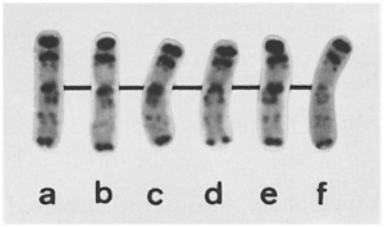


Fig. 2 a and b. Mitotic metaphase of a BC_1F_4-plant of the cross 'Cando' × 'Veery' in phase contrast (**a**) and after C-banding (**b**). (Secondary constrictions are marked with *arrows*)

cases they show a chromosome number of 2n = 28 and were homozygous for the *1BL/1RS* translocation, indicating that the translocation is cytologically stable. One plant was found showing a chromosome number of 2n = 28, which was homozygous for the *1BL/1RS* translocation; however, this plant was monosomic for chromosome *3A* and trisomic for *4B*, indicating that some cytological instability, especially in the *A*- and *B*-genome chromosome complement, might occur.

In phase contrast, only one chromosome pair shows a secondary constriction, and this pair can be identified after C-banding as being chromosome *6B* of wheat (Fig. 2). Furthermore, in all progenies homozygous for the *1BL/1RS* translocation, the maximum number of interphase nucleoli observed after Ag-NOR banding was two, indicating that only a pair of *6B* chromosomes was active in organizing nucleoli in this line.

In tetraploid (AABB) and hexaploid (AABBDD) wheats, two pairs of chromosomes show a secondary constriction at metaphase and these are known to be *1B* and *6B*. It is now well accepted that the secondary constrictions are the chromosomal sites of tandemly repeated genes coding for rRNA. Since these nucleolar organizer regions are very closely associated with the interphase nucleolus up to the end of prophase, they are less condensed than the rest of the chromatin, which leads to the formation of a secondary constriction and, depending on its location, to the formation of a satellite at metaphase. Thus, the presence of a secondary constriction at metaphase indicates that this region has shown nucleolar activity during the preceding interphase. In hexaploid wheat, 90% of the total rDNA genes is known to be located on *1B* (30%) and *6B* (60%) (Martini and



1BL/1RS translocation
, **a** 'Kronjuwel', **b** 'Dis-
' and **f** 'Heinrich'

Flavell 1985). An addition, chromosome *5D* is also active in organizing nucleoli; however, in this case usually no secondary constriction is formed. In diploid rye, only the short arm of chromosome *1R* carries rDNA gene cluster and shows a secondary constriction at metaphase (Miller et al. 1980).

The present results show that in the BC_1F_3- and BC_1F_4-plants homozygous for the *1BL/1RS* translocation, only chromosome pair *6B* is active in organizing nucleoli, while nucleolar activity of the rye segment *1RS* is suppressed. A similar suppression of NOR activity of *1RS* has been reported earlier for different wheat-rye hybrid combinations (Cermeño et al. 1984; Lacadena et al. 1984). However, there is some evidence that this suppression is not complete, as was shown by the occasional appearance of a dispersed state of rye rDNA in interphase nuclei revealed after in situ hybridization (Appels et al. 1986; Gustafson et al. 1988). In triticales with *A/B* mixed genomes missing both *1B* and *6B*, rye chromosome *1R* shows nucleolar activity as expressed by the capacity to organize nucleoli, by the presence of a sec-

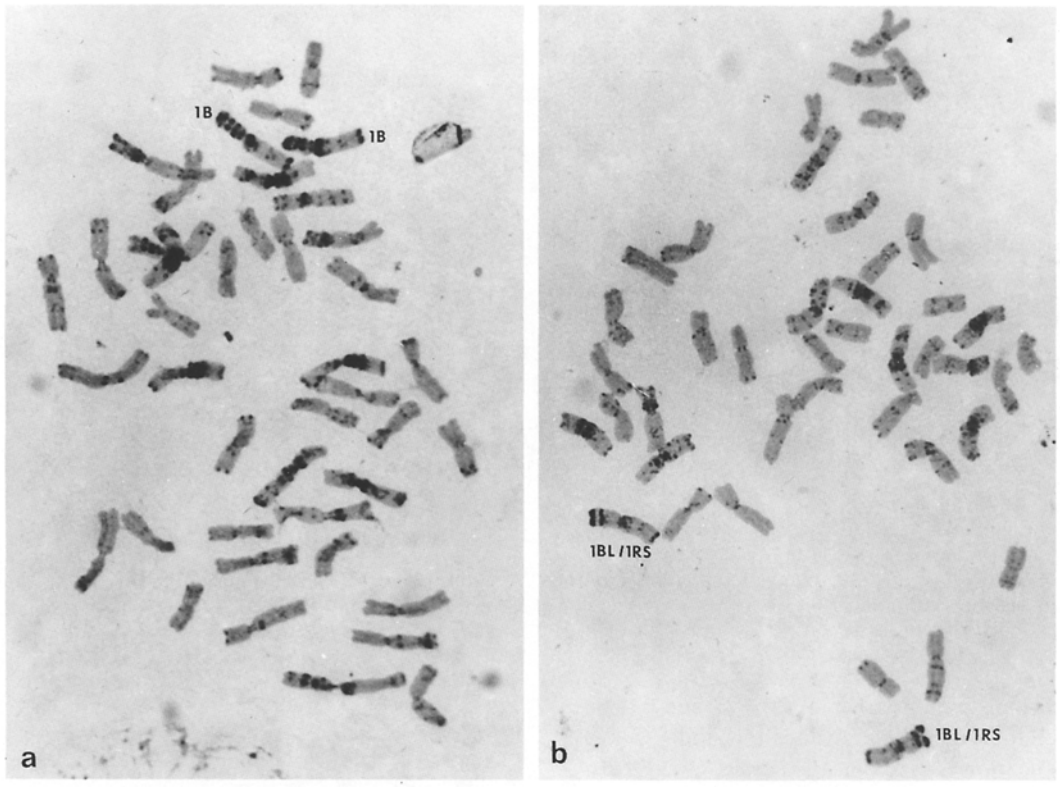


Fig. 4a and b. C-banded mitotic metaphases of the hexaploid wheat cultivars **a** 'Orbis' and **b** 'Olymp'

ondary constriction at metaphase and by the dispersed state of rye rDNA in interphase (Appels et al. 1986; Cermeño et al. 1987).

Figure 3 shows the C-banding pattern of the *1BL/1RS* wheat-rye translocation chromosomes present in the hexaploid wheat cultivars, 'Kronjuwel' (a), 'Disponent' (b), 'Götz' (c), 'Olymp' (d), 'Florida' (e) and 'Heinrich' (f). Complete C-banded metaphases of the cultivars 'Orbis' and 'Olymp' are given in Fig. 4. With the exception of the cultivar 'Orbis', which carries no *1BL/1RS* translocation, all of these lines are identical with respect to the C-banding pattern of the rye chromosome segment *1RS*.

Storage protein composition

Figure 5 shows single-seed PAGE patterns of the gliadins of 'Cando', 'Veery' and of the self-pollinated offspring of CV 256. Figure 6 presents the single-seed SDS-PAGE patterns of reduced glutenins of these lines.

Both 'Veery' and CV 256 were homozygous for the secalin-1 locus (Fig. 5, lanes 3 and 4), which is located on the short arm of rye chromosome *1R* (Lawrence and Shepherd 1981; Shewry et al. 1984). All seeds of CV 256 gave the same pattern as in lane 3. However, Fig. 6 shows that this material could be differentiated by the subunits produced by the *Glu-B1* locus, which is located on the long arm of chromosome *1B* of wheat (Payne 1987). The *Glu-B1* locus of 'Cando' produces the high molecular weight (HMW) glutenin subunits 6 and 8, while that of 'Veery' produces subunits 7 and 9 (Fig. 6). The CV 256 plants show segregation for these subunits. Whereas some plants show the parental-type pattern of 'Cando' (Fig. 6, lane 3) or 'Veery' (Fig. 6, lane 5), others show a mixture of both types (Fig. 6, lane 4), indicating that the material was heterozygous for that locus.

The segregation patterns observed for the *Glu-B1* HMW glutenin subunits can be explained by recombination events between the long arm of chromosome *1B* of 'Cando' and the *1BL* segment of the *1BL/1RS* translocation of 'Veery'. These chromosomes show homologous pairing in their long arms and usually form a rod bivalent at meiotic metaphase. Crossing-over between the centromere and the *Glu-B1* locus would lead to recombinants. The long arm of *1B* carries a marker band which is more pronounced in 'Cando' than in the *1BL/1RS* translocation of 'Veery' (Fig. 1). Since all BC_1F_4-plants analyzed were homozygous for the 'Veery'-type marker band of *1BL*, this indicates that the *GluB1* locus is distal to this marker band.

Expression of Pm8 resistance in tetraploid background

CV 256, along with the cultivars 'Disponent', 'Götz' and 'Veery', all carrying the *1BL/1RS* translocation, and

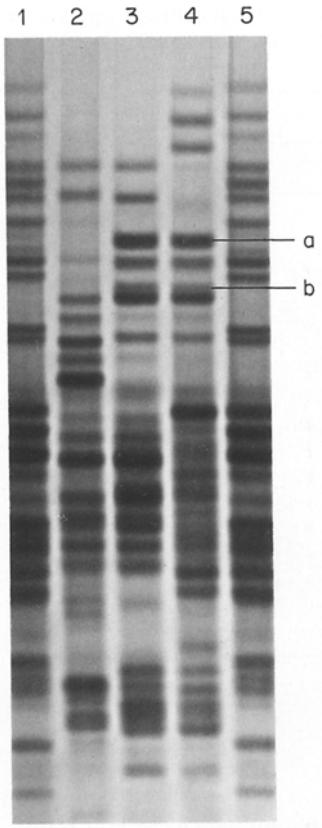


Fig. 5. Single-seed PAGE patterns (prolamins) of the wheat cultivars 'Neepawa' (*lane 1*; reference cultivar), 'Cando' (*lane 2*), BC_1F_4-seeds of the cross 'Cando' × 'Veery' (*lane 3*; five seeds gave the same patterns), 'Veery' (*lane 4*) and 'Neepawa' (*lane 5*); a and b highlight *1RS* bands

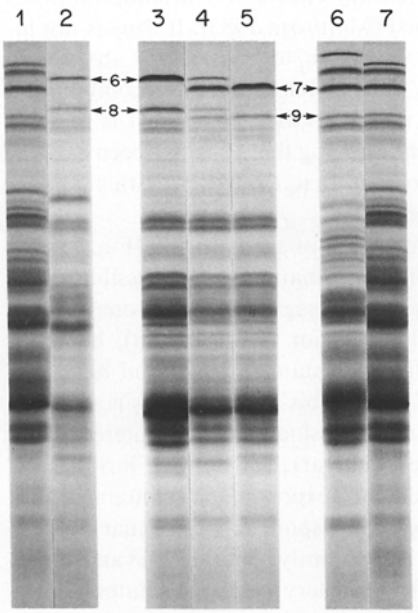


Fig. 6. Single-seed SDS-PAGE patterns (reduced glutenins) of the wheat cultivars 'Neepawa' (*lane 1*), 'Cando' (*lane 2*), BC_1F_4-seeds of the cross 'Cando' × 'Veery' (*lanes 3–5*), 'Veery' (*lane 6*) and 'Neepawa' (*lane 7*)

'Cando' were inoculated with *Pm8* avirulent powdery mildew isolates 6, 85135 and W72/27. All except 'Cando' gave mainly r reactions, indicating the presence of *Pm8* in 'Disponent', 'Götz' and 'Veery'. However, the powdery mildew isolates used are avirulent for *Pm3a* and *Pm3b*, and these genes could be responsible for the observed reaction with these three isolates. *Pm3a* and *Pm3b* avirulent powdery mildew isolates 2, 5 and 85063, which are virulent to *Pm8*, were chosen for the further inoculation experiments: 'Disponent', 'Götz' and 'Veery' were susceptible, CV 256 gave i or s reaction and the *Pm3a* and *Pm3b* carrier genotypes remained resistant (Table 1). The first three resistant reactions of CV 256 can be traced back to *Pm8*, and the fact that CV 256 reacts intermediate with two of the other powdery mildew isolates (nos. 2 and 85063) can be explained simply by the intermediate reactions of the female parent 'Cando' of that line. Thus, it is justified to conclude that the *Pm8* resistance, assumed to be located on *1RS*, is expressed in CV 256. In addition, this line possesses some powdery mildew resistance originating from 'Cando', as shown by the two intermediate reactions. But it should be added that 'Veery' also reacts resistant (r, i) with powdery mildew isolate no. 3 (characterized by Heun and Fischbeck 1987b) possessing virulence of *Pm8*, which holds also true for CV 256. Thus, we assume that 'Veery' is carrying *Pm8* plus some additional resistance, instead of only one unknown gene conditioning all the shown resistance patterns; experiments aiming to identify these additional resistance genes are in progress.

Expression of Pm8 resistance in hexaploid 1BL/1RS translocation lines

Translocation chromosome *1BL/1RS* was identified in several hexaploid German winter wheat cultivars (Fig. 3). All these cultivars are presumed to carry the *Pm8* gene located on *2RS* (McIntosh 1983). However, Heun and Fischbeck (1987a, b) have shown that 'Florida', 'Heinrich' and 'Olymp' do not express the *Pm8* gene. Thus, there is apparent discrepancy about the presence of the *1BL/1RS* translocation and the lack of *Pm8* gene expression in these three cultivars. In a repeated test, 'Florida' and 'Heinrich' again gave a highly susceptible reaction to all tested powdery mildew isolates, whereas *Pm8*-resistant cultivars 'Disponent' and 'Götz' showed typical resistance reactions (Table 1). 'Olymp' reacted identical with 'Orbis', which carries only *Pm4b*. The *Pm4b* gene does not disturb the expression of *Pm8*, as can be seen by the reaction of 'Kronjuwel' possessing *Pm4b* and *Pm8* (Heun and Fischbeck 1987a); both genes can be seen in this cultivar by their specific reaction (Table 1). Thus, it can be concluded that 'Florida', 'Heinrich' and 'Olymp' do not show *Pm8* resistance, whereas 'Disponent' and 'Götz' do.

Table 1. Powdery mildew reaction of 'Veery', CV256 and 'Cando' in comparison with the reaction of 17 wheat cultivars with known powdery mildew resistance, after inoculation with six different powdery mildew isolates (r = resistant, i = intermediate, s = susceptible, – = missing data)

Cultivar/near isogenic line	Resistance gene/s	Powdery mildew isolate no.					
		6	85135	W72/27	2	5	85063
'Axminster'/8CC[a]	*Pm1*	s	s	s	s	r	s
'Galahad'	*Pm2*	s	s	s	r	r	r
'Asosan'/8CC	*Pm3a*	i	i, r	r	r	r	r
'Chul'/8CC	*Pm3b*	r	r	r	r	r	r
'Sonora'/8CC	*Pm3c*	s	r	–	–	–	r
'Yuma'/8CC	*Pm4a*	s	s	r	s	i, r	s
'Orbis', 'Olymp'	*Pm4b*	s	s	r	s	r	s
'Rektor', 'Wattines'	*Pm5*[b]	i, s	i	i	s	s	s
'Disponent', 'Götz'	*Pm8*	r, i	r, i	r, i	s	s	s
'Mephisto'	*Pm9, 1, 2*	r	s	s	r	r	r
'Ralle'	*Mlk*	s	r	r	r	r	r
'Kronjuwel'	*Pm4b, 8*	r	r	r	s	r	s
'Florida'	–	s	s	s	s	s	s
'Heinrich'	–	s	s	s	s	s	s
'Veery'	*Pm8*	r	r	r	s	s	s
CV256	*Pm8, ?*	r	r	r	i	s	i
'Cando'	?	i, s	i	i	i	s	i

[a] Backcrossed eight times to 'Chancellor' (Briggle 1969)
[b] *Mli* is assumed to be identical with *Pm5* (Heun and Fischbeck 1987a, b)

To determine whether the *1BL/1RS* translocation in the above cultivars originates from the same source, pedigree relationships (G. Zimmermann, Personal communication) have to be taken into account.

'Florida' = 'Caribo' × 'Disponent'
'Heinrich' = 'Pantus' × 'Askro 3'
'Olymp' = (223/66 × 'Götz') × 'Kronjuwel'

'Askro 3' is derived from the cross 'Taca' × (SR × Wz). Wz is a wheat-rye bastard which has been used intensively in Weihenstephan, FRG, for breeding of rust-resistant wheat cultivars for over 30 years. Analyzing the pedigrees of well-known *Pm8* resistant cultivars (Zimmermann et al. 1984; Heun and Fischbeck 1987a), it becomes evident that all *1BL/1RS* translocations in the following West German wheat cultivars can be traced back to Wz line:

'Zorba' = (TC × SR × TC × CMr × Br) × Wz
'Benno' = 'Carstacht' × 'Zorba'
'Disponent' = ('Benno' × 'Florian') × 'Benno'
'Götz' = (('Tenor' × 'Jubilar') × 'Jubilar') × 'Benno'
'Kronjuwel' = ((14/48 × 465/52) × 353/49) × 'Caribo'

where 465/52 is (SR × AV × TSt) × Wz. 'Zorba' is a *1B/1RS* substitution line. Thus it is justified to conclude that the *1BL/1RS* translocation and the *1B/1R* substitution all may have been derived from Wz line. Consequently, the rye arm *1RS* has a single origin in all West German winter wheat cultivars mentioned above. The question as to why some of these cultivars carrying the *1BL/1RS* translocation are not expressing *Pm8* resistance cannot be answered by assuming different origins of that translocation.

There are several explainations as to why *Pm8* is not expressed in 'Olymp', 'Florida' and 'Heinrich' carrying *1BL/1RS:* First, it has never really been shown that *Pm8* is located on *1RS* (Lowry et al. 1984), although this has been widely assumed (McIntosh 1983). If *Pm8* is not located on *1RS,* it is simple to explain its absence in 'Olymp', 'Florida' and 'Heinrich' by recombination events. Second, if *Pm8* is located on *1RS,* it is possible that (a) the fragment carrying that gene has been lost, (b) a mutation occurred at that locus or (c) this gene is suppressed by other genes.

PAGE results for seven of the cultivars (Fig. 7) provided some additional information on the possible variation in the translocated *1RS* segment. All but one cultivar ('Orbis') contained the major *1RS* band (a), but only three, including 'Orbis', contained the second band (b). The origin of band b of 'Orbis' is not clear, since it does not have the *1BL/1RS* translocation. It is interesting to note that the three cultivars, 'Olymp', 'Florida' and 'Heinrich', which did not express *Pm8,* contained only band (a). In this regard, 'Disponent' was similar to these three cultivars, but it apparently contains *Pm8* and shows r, i reactions to the powdery mildew isolates nos. 6, 85135 and W72/27. work is in progress to determine unequivocally whether *Pm8* is located on *1RS* in an attempt to clarify the discrepancies noted herein. Since Koebner et al. (1986) reported about the transfer of stem

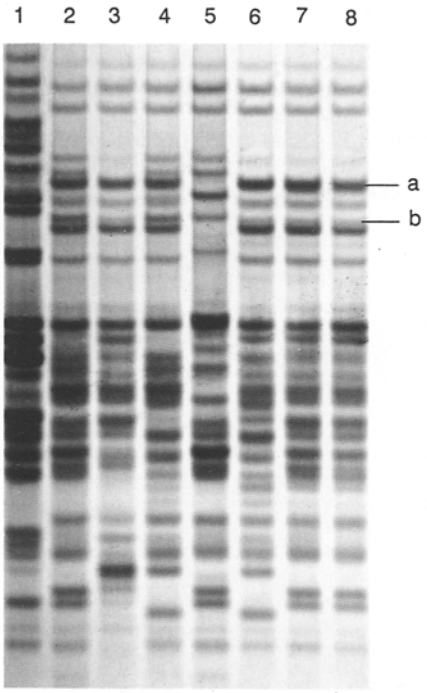


Fig. 7. Single-seed PAGE patterns of the hexaploid wheat cultivars 'Neepawa' (*lane 1*), 'Kronjuwel' (*lane 2*), 'Disponent' (*lane 3*), 'Götz' (*lane 4*), 'Orbis' (*lane 5*), 'Olymp' (*lane 6*), 'Heinrich' (*lane 7*) and 'Florida' (*lane 8*); *1RS* bands are identified as a and b

rust resistance from *1RS* to wheat chromosomes, we are also analyzing whether crossing-over between wheat and rye chromosome arms has occurred.

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References

Appels R, Moran LB, Gustafson JB (1986) The structure of DNA from the rye (*Secale cereale*) NOR R1 locus and its behaviour in wheat backgrounds. Can J Genet Cytol 28:673–685

Bennett FGA (1984) Resistance to powdery mildew in wheat: A review of its use in agriculture and breeding programs. Plant Pathology 33:279–300

Briggle LW (1969) Near-isogenic lines of wheat with genes for resistance to *Erysiphe graminis* f. sp. *tritici*. Crop Sci 9:70–72

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

Cermeño MC, Friebe B, Zeller FJ, Krolow K-D (1987) Nucleolar competition in different (A/B)(A/B)RR and DDRR tetraploid triticales. Heredity 58:1–4

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. Proc 6th Intern Wheat Genet Symp, Kyoto, 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

Friebe B, Zeller FJ, Kunzmann R (1987) Transfer of the 1BL/1RS wheat-rye translocation from hexaploid bread wheat to tetraploid durum wheat. Theor Appl Genet 74:423–425

Gill BS (1987) Chromosome banding methods, standard chromosome band nomenclature and applications in cytogenetic analysis. In: Heyne EG (ed) Wheat and wheat improvement. Am Soc Agron Inc. Madison, 243–254

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

Gustafson JP, Dera AR, Petrovic S (1988) Expression of modified rye ribosomal RNA genes in wheat. Proc Natl Acad Sci USA 85:3943–3945

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

Iordanski AB, Zurabishvili TB, Badaev NS (1978) Linear differentiation of cereal chromosomes. 1. Common wheat and its supposed ancestors. Theor Appl Genet 51:145–152

Koebner RMD, Shepherd KW, Appels R (1986) Controlled introgression to wheat of genes from rye chromosome arm 1RS by induction of allosyndesis. 2. Characterization of recombinants. Theor Appl Genet 73:209–217

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

Lawrence GJ, Shepherd KW (1981) Chromosomal location of genes controlling seed proteins in species related to wheat. Theor Appl Genet 59:25–31

Lowry JR, Sammons DJ, Baenzinger PS, Moseman JG (1984) Identification and characterization of the gene conditioning powdery mildew resistance in 'Amigo' wheat. Crop Sci 24:129–132

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

Martini G, Flavell RB (1985) The control of nucleolus volume in wheat: a genetic study at three developmental stages. Heredity 54:111–120

McIntosh RA (1983) A catalogue of gene symbols for wheat. In: Sakamoto S (ed) Proc 6th Intern Wheat Genet Symp Plant Germ-Plasm Inst. Fac. Agric, Kyoto, pp 1197–1255

Merker A (1982) 'Veery' a CIMMYT spring wheat with the 1BL/1RS translocation. Cereal Res Commun 10:105–106

Mettin D, Blüthner W-D (1984) Zur gegenwärtigen Verbreitung des Roggenchromosoms 1R im Weizenzuchtmaterial der DDR. Tagungsber Akad Landwirtschaftswiss DDR 224:527–534

Miller TE, Gerlach WL, Flavell RB (1980) Nucleolus organizer variation in wheat and rye revealed by in situ hybridization. Heredity 45:377–382

Ng PKW, Bushuk W (1987) Glutenin of Marquis wheat as a reference for estimating molecular weights of glutenin sub-

units by sodium dodecyl sulfate-polyacrylamide gel electrophoresis. Cereal Chem 64:324–327

Payne PI (1987) Genetics of wheat storage proteins and the effects of allelic variation on bread-making quality. Annu Rev Plant Physiol 38:141–153

Sapirstein HD, Bushuk W (1985) Computer-aided analysis of gliadin electrophoregrams. I. Improvement of precision of relative mobility determination by using a three reference band standardization. Cereal Chem 62:372–377

Shewry RP, Bradberry D, Franklin J, White RP (1984) The chromosomal locations and linkage relationships of the structural genes for the prolamine storage proteins (secalins) of rye. Theor Appl Genet 69:63–69

Zeller FJ, Fuchs E (1983) Cytologie und Krankheitsresistenz einer 1A/1R- und mehrerer 1B/1R-Weizen-Roggen-Translokationen. Z Pflanzenzuecht 90:285–296

Zimmermann G, Wenisch K, Strass F (1984) Further results of attempts to combine mildew resistance in winter wheat. Vortr Pflanzenzuecht 6:85–102