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Electrophoretic protein analysis for the identification of doubled haploid 1A-1R, 1B-1R wheat-rye double translocation lines and for the assessment of their genetic stability

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Abstract. Eighteen available doubled haploid wheat lines with a cytologically proven 1A-1R, 1B-1R double translocation, which where derived via anther culture from four crosses of the 1A-1R wheat-rye translocation cv "Amigo" with several 1B-1R wheat-rye translocation forms, were subjected to electrophoretic seed protein analysis. Besides, the five parents used in the crosses and some other wheat cultivars and doubled haploid lines (19 with a 1B-1R single translocation, 10 with a 1A-1R translocation and 7 without any 1R translocation) were also included in the investigation. It was found that the gliadin patterns visualized after SDS polyacrylamide gel electrophoresis of alcohol-soluble seed protein extracts can differentiate not only 1B-1R and 1A-1R translocation forms from wheats without any 1R-translocation chromosome, but also 1B-1R and 1A-1R wheats from each other. Moreover, 1A-1R, 1B-1R double translocation lines can be distinguished as well due to characteristic differences revealed between 1A-1R and 1B-1R translocation forms. Thus, all of tested dh_1- and dh_2-grains of the double translocation lines showed the expected doublet: the 1A-1R translocation ("Amigo")-typical rye band and the 1B-1R translocation ("Kawkas")-typical rye band. Consequently, gliadin patterns estimated after SDS electrophoresis may be used as markers for the fast detection of the desired 1A-1R, 1B-1R double translocation forms among 1A-1R single translocation lines, 1B-1R single translocation lines and lines without any 1R-translocation in the progenies of appropriate crosses. Furthermore, by means of gliadin tests on the dh_2-generation the excellent stability of the double translocation 1A-1R, 1B-1R during more than one propagation phase has been proven. Estimations of high-molecular weight (HMW) glutenin subunits coded by 1A and 1B chromosomes are compatible with the double translocation constitution. A few deviating results can be explained by crossing-over events. Seed protein analysis revealed that it is possible to produce 1A-1R, 1B-1R double translocation lines with good glutenin compositions provided that adequate favourable parents are used.

Key words: Gliadin – HMW glutenin – SDS electrophoresis – Biochemical marker – 1A-1R, 1B-1R wheat-rye double translocation – Doubled haploids – *Triticum aestivum L.*

Introduction

Wheats with a 1BL-1RS wheat-rye translocation chromosome have been known about for a long time and are widespread (e.g. Mettin et al. 1973; Zeller 1973; Zeller and Fuchs 1983; Mettin and Blüthner 1984; Vahl and Müller 1984, 1986; Gustafson 1988; Lookhart et al. 1991). In 1976 'Amigo' was released as the first 1AL-1RS wheat-rye translocation cultivar (Sebesta and Wood 1978). In crosses between wheats with a 1BL-1RS translocation and the wheat cv 'Amigo' lines can be obtained in which the short arm of the 1R rye chromosome (1RS) is present in quadruple; i.e. two 1BL-1RS chromosomes and two 1AL-1RS chromosomes exist. These lines should be of interest to geneticists and breeders alike (Zeller and Fuchs 1983). The production of such 1A-1R, 1B-1R double translocation wheats quickly succeeded owing to the use of the anther culture haploid technique (Müller et al. 1990).

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Until now the selection of doubled haploid (dh-)lines with a double translocation has been mainly based on the results of cytological analysis: the 1A-1R chromosome pair and the 1B-1R chromosome pair in root-tip metaphase cells of progenies (dh_1-lines) of the doubled anther culture regenerate plants have to be demonstrated by Giemsa-C-banding (Müller et al. 1990; Böhme et al. 1991). The substitution of this relatively expensive differential chromosome staining technique by a more simple and quick method for detecting haploids or dh-lines with the double translocation, such as a biochemical marker, would be desirable.

In previous investigations in which wheats without any 1R-translocation were crossed with wheats with a 1B-1R translocation or a 1A-1R translocation the electrophoretic patterns of peroxidase are judged to be suitably adequate to differentiate between the new developed pollen plants with the 1B-1R or the 1A-1R translocation chromosome and the regenerates with "normal" wheat chromosomes 1A and 1B (Müller et al. 1989 a, b). However, upon the hybridization of 1A-1R translocation wheats and 1B-1R translocation wheats, multiple peroxidases were observed to be only valid for discrimination of anther culture descendants (a) without a translocation and (b) with a 1A-1R single translocation from (c) a group of regenerates with either a 1B-1R single translocation or a 1A-1R, 1B-1R double translocation. At best both forms of group c can be distinguished by differences in the intensity of the 1RS-coded peroxidase, which should be present in wheats with a double translocation in a two-fold dose in comparison to the single translocation 1B-1R. But even if the expression of the 1R-coded peroxidase correlates strictly with the dosage of the 1RS chromosome arm, such quantitative differences in multiple enzyme patterns can hardly be used in routine analysis. For this reason it is necessary to involve more proteins located on rye chromosome 1R or on the wheat chromosomes of homoeologous group 1 in the biochemical analysis of the 1A-1R, 1B-1R double translocation to test the possibility of using these other proteins for distinguishing lines with a 1B-1R single translocation from lines with a 1A-1R, 1B-1R double translocation.

First of all the glucosephosphate isomerase and gliadins encoded by the short arms of chromosomes 1A, 1B, 1D and 1R, respectively, should be investigated for their potential to reflect the substitution of the 1AS or (and) 1BS arm by 1RS. However, glucosephosphate isomerase has been found not to be able to differentiate the 1B-1R single translocation from the 1A-1R, 1B-1R double translocation because of the subunit composition and distribution of this dimeric enzyme (U. Vahl and G. Müller, unpublished).

In the present article, we present our results on the suitability of gliadin proteins to be biochemical markers for the presence of the 1A-1R, 1B-1R double translocation in wheat. Furthermore, preliminary data on the genetic stability of the double translocation based on a gliadin analysis of seeds originating from self-pollinated microspore-derived plants are presented. Although the high-molecular-weight (HMW) glutenins are located on the long arms of chromosomes 1A, 1B, 1D and 1R and thus are not able to reflect the exchange of 1AS and 1BS chromosome arms by the 1RS arm, they are also analysed since the long arms 1AL and 1BL are also involved in the 1AL-1RS and 1BL-1RS translocations. Moreover, the glutenin composition of the 1AL-1RS, 1BL-1RS double translocation forms is of interest because of its importance for wheat quality.

Table 1. Breeding schemes of the four F_1 populations used in anther culture to produce the doubled haploid winter wheat lines analysed by protein electrophoresis (Table 2)

Population		Female parent		Male parent
E87/5	=	Amigo	×	TAW 5.24743/79
E87/6	=	Amigo	×	Iris
E87/145	=	Kawkas	×	Amigo
KHK 7	=	Ikarus	×	Amigo

Materials and methods

Plant material

The analysed material mainly consisted of the doubled haploid lines (Table 2) obtained from four F_1 populations that originated from crosses between the 1A-1R translocation cultivar 'Amigo' and various 1B-1R translocation wheats (Table 1). These lines have been characterized cytologically as 1A-1R, 1B-1R double translocation lines (Müller et al. 1990; Böhme et al. 1991). In some cases we also analysed clones to verify the results. The dh_1-lines, i.e. the kernels produced by the dh_0-plants (doubled anther culture regenerate plants) were the primary material studied, but sometimes their progenies, i.e. the dh_2-caryopses, were also examined. For comparison purposes some dh-lines originating from the same populations but which only a single translocation, 1A-1R or 1B-1R, according to the cytological data (Table 2), and several wheat cultivars and breeding lines with a known 1B-1R or 1A-1R translocation (Table 3), for instance the parents of our four F_1 populations, were also analysed.

Electrophoretic procedures

Protein analysis was carried out mainly on single seeds, sometimes on half seeds. As a rule, 500 µl of the extraction medium was added to one whole pounded grain; accordingly, 250 µl to a half kernel.

For gliadin fractionations the seeds were extracted with 70% ethanol overnight. After centrifugation the supernatant was evaporated, dissolved in an aliquot volume of TRIS-HCL buffer (pH 6.8) containing 2% SDS and then separated by SDS polyacrylamide gel electrophoresis (PAGE) modifying the protocol of Laemmli (1970) by using separation gels of 10% acrylamide and 0.3% BIS and stacking gels of 5% acrylamide and 0.8% BIS. The gels were run at 200 V. After about 2.5 h the bromphenol blue marker dye had reached a position about 1 cm from the lower end of the gel, but separation still continued for 30 min. The SDS gels were stained with a solution of 0.025% Coomassie BrilliantBlueR250 in trichloracetic acid (20%):methanol: acetic

Table 2. Classification of some dh_1-lines with respect to their type of wheat-rye translocation by means of gliadin analysis after SDS-PAGE of alcohol-soluble seed storage proteins and to their HMW glutenin composition obtained by SDS-PAGE of reduced total seed storage protein extracts

Wheat dh_1-line, its donor population[a] and translocation type[b]			Rye chromosome bands observed in the gliadin patterns			HMW glutenin subunits observed			
			1BL-1RS (Kawkas)-typical 1RS-coded protein	1AL-1RS (Amigo)-typical 1RS-coded protein	Number of caryopses tested	1A	1B	1D	Number of caryopses tested
887	E87/145	not translocated	−	−	2	N	7+ 9	5+10	1
1503	KHK7	not translocated	−	−	2	N	7+ 9	5+10	3
457	E87/5	1BL-1RS	+	−	1	N	17+18	2+12	2
494	E87/5	1BL-1RS	+	−	1	N	17+18	5+10	2
917	E87/5	1BL-1RS	+	−	1	N	17+18	2+12	1
195	E87/5	1BL-1RS	+	−	3	N	7+ 9	5+10	4
811	E87/6	1BL-1RS	+	−	2	N	7+ 9	5+10	2
276	E87/145	1BL-1RS	+	−	2	N	7+ 9	5+10	1
830	E87/145	1BL-1RS	+	−	2	N	7+ 9	5+10	1
446	E87/145	1BL-1RS	+	−	1	N	7+ 9	5+10	1
637	E87/145	1BL-1RS	+	−	2	N	7+ 9	5+10	1
1478	KHK7	1BL-1RS	+	−	2	N	6+ 8	5+10	3
1489	KHK7	1BL-1RS	+	−	2	N	6+ 8	5+10	3
351	E87/5	1AL-1RS	−	+	3	2*	7+ 9	5+10	3
390	E87/5	1AL-1RS	−	+	2	2*	7+ 9	5+10	3
892	E87/5	1AL-1RS	−	+	3	2*	7+ 9	5+10	4
348	E87/6	1AL-1RS	−	+	2	2*	7+ 9	5+10	1
742	E87/145	1AL-1RS	−	+	2	2*	7+ 9	5+10	1
410	E87/145	1AL-1RS	−	+	1	2*	7+ 9	5+10	1
906	E87/145	1AL-1RS	−	+	2	2*	7+ 9	5+10	1
285	E87/145	1AL-1RS	−	+	4	2*	7+ 9	5+10	1
1480	KHK7	1AL-1RS	−	+	2	2*	7+ 9	5+10	3
1067	E87/5	DT[c]	+	+	4	N	17+18	5+10	4
1067[d]	E87/5	DT	+	+	16	N	17+18	5+10	8
667	E87/5	DT	+	+	1	2*	17+18	5+10	2
552	E87/5	DT	+	+	1	2*	17+18	5+10	2
573	E87/5	DT	+	+	1	2*	17+18	5+10	2
532	E87/6	DT	+	+	14	2*	7+ 9	5+10	12
419	E87/6	DT	+	+	11[e]	N	7+ 9	2+12	16
419[d]	E87/6	DT	+	+	43[f]	N	7+ 9	2+12	25
191[d]	E87/145	DT	+	+	16	2*	7+ 9	5+10	4
442[d]	E87/145	DT	+	+	10	2*	7+ 9	5+10	4
425[d]	E87/145	DT	+	+	8	2*	7+ 9	5+10	4
980[d]	E87/145	DT	+	+	8	2*	7+ 9	5+10	4
727	E87/145	DT	+	+	2	2*	7+ 9	5+10	2
914	E87/145	DT	+	+	2	2*	7+ 9	5+10	2
915	E87/145	DT	+	+	2	2*	7+ 9	5+10	2
518	E87/145	DT	+	+	1	2*	7+ 9	5+10	1
483	E87/145	DT	+	+	1	2*	7+ 9	5+10	1
693	E87/145	DT	+	+	1	2*	7+ 9	5+10	3
484	E87/145	DT	+	+	1	2*	7+ 9	5+10	3
1481	KHK7	DT	+	+	2	2*	6+ 8	5+10	2
1481[d]	KHK7	DT	+	+	99	2*	6+ 8	5+10	21

+, Protein present; −, protein absent

[a] According to populations of Table 1

[b] According to peroxidase marker and/or cytological data

[c] DT, Double translocation 1AL-1RS, 1BL-1RS

[d] Dh_2 instead of dh_1 kernels are analysed

[e] 'Amigo'-typical 1R-coded gliadin is absent in 1 of the tested caryopses

[f] 'Amigo'-typical 1R-coded gliadin is absent in 10 of the tested caryopses

Table 3. Classification of some wheat cultivars and breeding lines with respect to their type of wheat-rye translocation by means of gliadin analysis after SDS-PAGE of alcohol-soluble seed storage proteins and to their HWM glutenin composition obtained by SDS-PAGE of reduced total seed storage protein extracts

Wheat form and its translocation type[a]		Rye chromosome bands observed in the gliadin patterns			HMW glutenin subunits observed			
		1BL-1RS (Kawkas)-typical 1RS-coded protein	1AL-1RS (Amigo)-typical 1RS-coded protein	Number of caryopses tested	1A	1B	1D	Number of caryopses tested
Alcedo	not translocated	–	–	>100	N	7+ 9	5+10	27
Zentos	not translocated	–	–	11	N	7+ 9	5+10	21
Alidos	not translocated	–	–	10	N	17+18	5+10	34
Borenos	not translocated	–	–	9	N	7+ 9	2+12	27
C. Spring	not translocated	–	–	14	N	7+ 8	2+12	13
Kawkas[b]	1BL-1RS	+	–	>100	N	7+ 9	5+10	30
Solaris	1BL-1RS	+	–	10	1	7+ 9	5+10	50
Ikarus[b]	1BL-1RS	+	–	12	N	6+ 8	5+10	25
Olymp	1BL-1RS	+	–	6	N	6+ 8	5+10	16
Knirps	1BL-1RS	+	–	9	N	7+ 8	2+12	19
Zombor	1BL-1RS	+	–	8	N	7+ 9	2+12	34
Iris[b]	1BL-1RS	+	–	17	N	7+ 9	2+12	29
Apollo	1BL-1RS	+	–	4	N	6+ 8	2+12	26
Sleipner	1BL-1RS	+	–	3	N	6+ 8	2+12	13
Hornet	1BL-1RS	+	–	1	N	6+ 8	2+12	11
Palur	1BL-1RS	+	–	6	N	13+19	2+12	28
5.24743[b]	1BL-1RS	+	–	5	N	17+18	2+12	17
Amigo[b]	1AL-1RS	–	+	89	2*	7+ 9	5+10	75
Century	1AL-1RS	–	+	10	2*	7+ 9	5+10	22

+, Protein present; –, protein absent
[a] According to peroxidase marker and/or cytological data
[b] Used as crossing parents in Table 1

acid:water (30:20:7:50) overnight and then shaken in a solution of methanol:acetic acid:water (6:1:14) until the underground had destained.

To estimate HMW glutenin patterns the reduced total protein was extracted with TRIS-HCL buffer (pH 6.8) containing 2% SDS and 5% β-mercaptoethanol (Laemmli 1970) overnight. After centrifugation the extracts were separated by SDS electrophoresis. As a rule, running gels with 15% acrylamide and 0.075% BIS were used. In particular cases gels with 7.5% acrylamide and 0.3% BIS served for separation purposes because these larger-pore gels give a better resolution of HMW glutenin subunits 2 and 2* (Payne et al. 1987). The 15% gels were subjected to electrophoresis at 200 V for about 2–2.5 h during which time the tracking dye bromphenolblue arrived at the bottom of the gel. The electrophoresis was then allowed to continue for 5 h. When 7.5% gels were used, electrophoretic separation continued only for 1.5 h. The glutenin subunits were visualized as described for gliadins and are designated following Payne et al. (1980) and Payne and Lawrence (1983).

Results and discussion

The gliadin patterns of wheats with a single 1BL-1RS- or a single 1AL-1RS translocation

The patterns of alcohol-soluble seed storage proteins of the 1BL-1RS wheat-rye translocation cvs 'Kawkas', 'Solaris', 'Ikarus', 'Olymp', 'Knirps', 'Zombor', 'Iris', 'Apollo', 'Sleipner', 'Hornet', 'Palur' and 'TAW 5.24743/79' separated by SDS-PAGE are different from those of wheat cultivars without any 1RS-translocation, such as 'Alcedo', 'Zentos', 'Alidos', 'Borenos' and 'Chinese Spring' (Fig. 1 and Table 3). This finding is in accordance with the results of other authors who also applied SDS separation technique to detect the 1BL-1RS translocation by means of characteristic gliadins (Petrovic et al. 1988; Koebner and Shepherd 1986; Graybosch et al. 1990; Lookhart et al. 1991), not to mention the great number of working groups using acid polyacrylamide gel electrophoresis for gliadin analyses.

The 1BS-coded gliadins are absent in the 1BL-1RS translocation wheat cultivars; these are always present in normal wheats like 'Borenos', 'Chinese Spring' and 'Alcedo', and are denoted in the patterns of these cultivars in Fig. 1 with arrows. Instead of 1BS-dependent gliadins 1RS-coded proteins are visible, particularly the relatively strong band that is marked in the patterns of the 1BL-1RS translocation wheats of Fig. 1 by a cross; this band is labelled as a 'Kawkas'-typical 1RS-coded rye gliadin (Table 3). This characteristic substitution of wheat

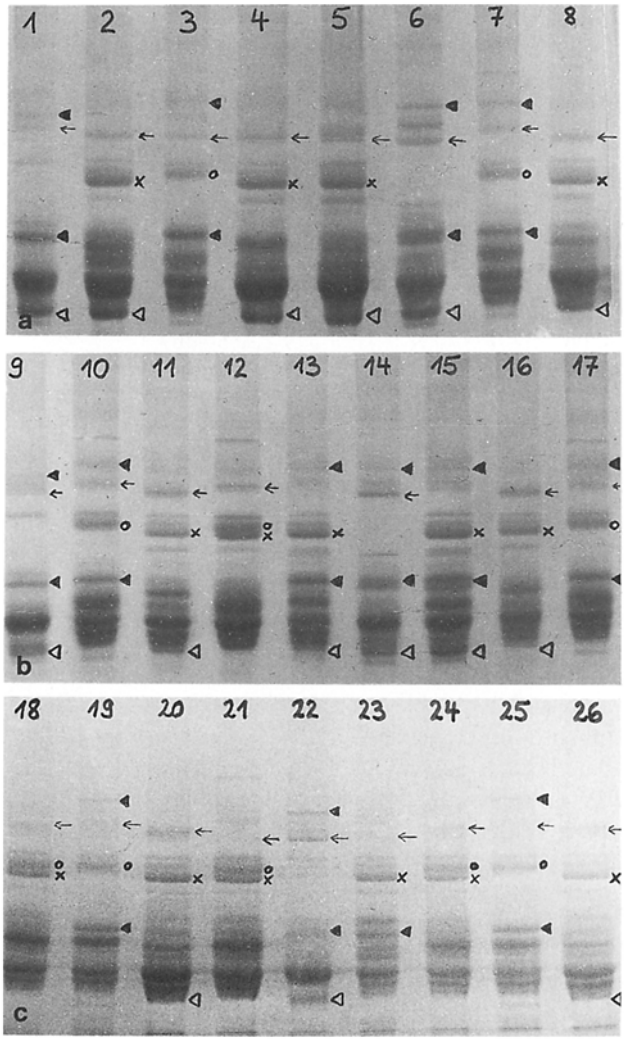

Fig. 1. SDS-PAGE patterns of alcohol soluble seed proteins of several wheats with different constitutions with respect to the 1RS-translocation in comparison to normal wheats without any translocation. Figure 1 represents several gel plates; separating gel: 10% acrylamide. *1* 'Borenos', *2* 'Hornet' 1BL-1RS, *3, 25* 'Century' 1AL-1RS, *4* 'Palur' 1BL-1RS, *5* 'Ikarus' 1BL-1RS, *6, 14* 'Chinese Spring', *7, 10, 17, 19* 'Amigo' 1AL-1RS, *8, 20, 26* 'Kawkas' 1BL-1RS, *9, 22* 'Alcedo', *11* 'TAW 5.24743/79' 1BL-1RS, *12, 21* DT 1AL-1RS, 1BL-1RS dh_2 1067, *13* 1DL-1RS 'Gabo', *15* 1DL-1RS 'Chinese Spring', *16* 'Iris' 1BL-1RS, *18, 23* DT 1AL-1RS, 1BL-1RS dh_2 419, *24* DT 1AL-1RS, 1BL-1RS dh_2 980. ◁ 1AS-coded wheat gliadin, ◀ 1BS-coded wheat gliadin, ← 1DS-coded wheat gliadin, o 1RS-coded rye protein in 1AL-1RS translocation wheat 'Amigo' and descendants (derived from 'Insave' rye), × 1RS-coded rye protein in 1BL-1RS translocation wheat 'Kawkas' and descendants (derived from 'Petkus' rye) and in 'Chinese Spring' 1DL-1RS translocation and descendants (derived from 'Imperial' rye), respectively.

gliadins by rye gliadins could be an useful tool to detect the presence of the 1BL-1RS translocation in all wheats.

This is confirmed by SDS-PAGE analysis of alcohol-soluble seed storage proteins of the dh-lines derived from the F_1 populations E87/5, E87/6, E87/145 and KHK7, and therefore based on crosses with the 1B-1R translocation forms 'TAW 5.24743/79', 'Iris', 'Kawkas' and 'Ikarus', respectively (Table 1). All of the anther culture progenies with the 1B-1R translocation chromosome according to the peroxidase test and/or cytological data show the above-described deviating pattern with the 'Kawkas'-typical rye band that indicates the presence of the 1B-1R chromosome (compare dh_1 457, 494, 917, 195 from E87/5, dh_1 811 from E87/6, dh_1 276, 830, 446, 637 from E87/145 and dh_1 1478, 1489 from KHK7 in the Table 2). On the contrary, those dh-lines also derived from these crosses but without the 1B-1R translocation (e.g. dh_1 887 from E87/145 and dh_1 1503 from KHK7) possess normal gliadin patterns without the rye gliadin bands (Table 2).

The 1AL-1RS translocation can also be reflected by means of rye-typical gliadins. This has been revealed for the cv 'Amigo' and an 'Amigo'-derived wheat line after separation of ethylene glycol extracts by acid PAGE (Berzonsky et al. 1991) and for a "Chinese Spring"-"Hope"-1AL-1RS translocation line after fractionation of total protein extracts by SDS electrophoresis (Singh and Shepherd 1988).

Figure 1 shows that the SDS polyacrylamide gel patterns of alcohol-soluble seed proteins are also suitable for the identification of the 1AL-1RS translocation. For example, in the 1AL-1RS translocation wheat cv 'Amigo' the 1AS-coded gliadin is absent while additional rye bands occur. The most characteristic rye gliadin is marked by a circle. It has a slightly slower mobility than the corresponding rye protein ('Kawkas'-typical band) of the 1BL-1RS translocation wheats mentioned above. This difference is probably due to the presence of different gliadin alleles at the 1R chromosomes of the Argentine rye 'Insave' from which 'Amigo' is derived and of the German rye 'Petkus' from which 1B-1R translocation wheats like 'Kawkas', 'Iris' etc. originate. Another possible explanation could be that the translocation in 'Amigo' and 'Kawkas' involves the different chromosomes 1A and 1B, which may variously influence the expression of rye genes (Berzonsky et al. 1991). To distinguish the 'Kawkas'-typical rye band of the 1B-1R translocation wheats from the slower-moving rye gliadin of the 1A-1R translocation wheat cv 'Amigo' we have named the latter the 'Amigo'-typical rye band (cp. Table 3).

According to peroxidase tests and cytological results several of the dh-lines derived from the crosses with 'Amigo' (Table 1) represent further 1A-1R translocation forms (Table 2), and these are available for examining the common occurrence of the deviating gliadin pattern relative to the 1B-1R translocation wheats. In all nine doubled haploid 1A-1R translocation lines tested by means of SDS-PAGE of alcohol-soluble seed protein extracts, the 'Amigo'-typical patterns with the characteristic slower-moving rye band are observed. In Table 2 this is demonstrated for dh_1 351, 390, 892 from the F_1 popula-

tion E87/5, for dh_1 348 from E87/6, for dh_1 742, 410, 906, 285 from E87/145 and for dh_1 1480 from KHK7.

In the cv 'Century', released to growers in 1986, the gliadin patterns characteristic of "Amigo" and its derived dh-lines with a 1A-1R translocation are also observed (Fig. 1, Table 3). 'Century' descends from the cross 'Payne'//'TAM W 101'/'Amigo' and carries, like 'Amigo', resistance to biotype C of the greenbug, which originates from 'Insave' rye (Smith et al. 1989) and has been localized in 'Amigo' on the 1AL-1RS translocation chromosome (Hollenhorst and Joppa 1981; Zeller and Fuchs 1983).

From these facts it could be supposed that the 1A-1R translocation has been transferred from 'Amigo' to 'Century'. This expectation has found its first confirmation by means of the described gliadin patterns. In addition, the estimation of multiple leaf peroxidases according to our previous investigations corroborates the same phenotype AB that is typical of the 1AL-1RS translocation wheat 'Amigo' (Müller and Vahl 1986, Müller et al. 1989b) in 'Century' (U. Vahl and G. Müller, unpublished). Likewise, the presence of the 1A-1R translocation chromosome in 'Century' could be verified by Giemsa-C-banding (T. Böhme, unpublished). The presence of the 1A-1R translocation in this variety is also mentioned by Lookhart et al. (1991).

Although wheats with a 1DL-1RS-translocation are not the objects of investigation it should be mentioned that they may be differentiated in an analogous way as the 1A-1R- and 1B-1R wheats. In the alcohol-soluble seed protein patterns obtained upon SDS electrophoresis of 1D-1R-'Warigal', 1D-1R-'Gabo' and 1D-1R-'Chinese Spring', the 1DS-coded wheat gliadin is absent. Instead, a 1RS-coded rye protein can be observed. The mobility of this additional rye protein corresponds to that of the 1BL-1RS translocation ('Kawkas')-typical rye gliadin and differs from that of the 1AL-1RS translocation ('Amigo')-typical rye gliadin (compare with 1D-1R-'Gabo' and 1D-1R-'Chinese Spring' in Fig. 1)[1].

Gliadin analysis of 1A-1R, 1B-1R double translocation lines

The differences in the electrophoretic patterns of the alcohol-soluble seed storage proteins of the 1A-1R translocation wheat 'Amigo' and its descendants and in those of the 1B-1R translocation wheat cultivars and breeding lines (Fig. 1, Table 2, 3 and described above) should make it possible to distinguish 1A-1R, 1B-1R double translocation lines by means of gliadin patterns separated by SDS electrophoresis. These forms are discernible by the absence of both 1A- and 1B-coded wheat proteins as well as by the presence of both 'Amigo'-typical and 'Kawkas'-typical 1R-coded rye proteins.

In the 18 dh-lines with a cytologically proven 1A-1R, 1B-1R double translocation (Table 2, dh 1067 ... dh 1481), such patterns are found. In Fig. 1, where three double translocation lines, dh_2 1067, dh_2 419 and dh_2 980 are demonstrated, it is evident that the simultaneous presence of the 1A-1R and 1B-1R chromosomes in wheat is well reflected in gliadin patterns. The characteristic doublet, consisting of the two rye proteins (the slower migrating gliadin, marked by a circle, originates from the 1A-1R translocation wheat 'Amigo'; the faster moving gliadin, marked by a cross, is attributed to the 1B-1R translocation wheats 'Kawkas', 'Iris' or 'TAW 5.24743/79'), is especially visible. The doublet of the additional rye bands as well as the missing 1A- and 1B-coded wheat bands have also been observed in all of the other 15 dh-lines with a double translocation that are available at present (Table 2). These data indicate that 1A-1R, 1B-1R double translocation lines can be very precisely identified on the basis of electrophoretic gliadin patterns. The quantity of seeds tested for each doubled haploid double translocation line is also given in Table 2. On reflection it turns out that all of the seeds of every line (except of dh 419) homogeneously show the pattern typical of wheats with both a chromosome 1A-1R and a chromosome 1B-1R. Thus, it appears that the 1A-1R, 1B-1R double translocation is relatively stable. The 99 dh_2-caryopses of line 1481, which all exhibit the rye band doublet, particularly supports this conclusion.

Only in the progeny of dh-line 419 did some seeds obviously not possess the 1A-1R chromosome (Fig. 1, also see the annotation to dh 419 in Table 2). Because the absence of the 'Amigo'-typical 1R-coded rye protein could be observed in the dh_1-generation it is more probable that in dh 419 a chromosomal disturbance is present from the beginning rather than that the 1A-1R chromosome is lost again. Thus, our assertion about the good stability of the 1A-1R, 1B-1R double translocation lines is sustained despite the somewhat irregular results of dh 419.

The HMW glutenin subunit composition of the analysed material

The other protein group traditionally recognized in the wheat grain, the HMW glutenin subunits are controlled by the long arms of homoeologous group-1 wheat chromosomes and rye chromosome 1R and therefore can not be modified by the 1AL-1RS- and/or by the 1BL-1RS-

[1] After this manuscript had been prepared for publication we became aware of the paper by Gupta and Shepherd "Identification of rye chromosome 1R translocations and substitutions in hexaploid wheats using storage proteins as genetic markers", Plant Breed 109:130–140 (1992), in which similar results are revealed by means of SDS-PAGE of unreduced total seed proteins

translocation. However, the 1AL-1RS, 1BL-1RS double translocation lines should be estimated based on their electrophoretic glutenin patterns. These are two reasons for our interest: (1) the importance of glutenins in the processing of wheat into its food products and (2) the differences in HMW glutenins that are shown by the parents of our four crosses E87/5, E87/6, E87/145 and KHK7. Table 3 summarizes the latter point and shows HMW glutenin subunit compositions in cultivars with a 1B-1R- or 1A-1R translocation that have been tested in the gliadin analyses.

A nearer consideration reveals that all of the 1B-1R translocation forms used in our crosses ('Kawkas', 'Iris', 'Ikarus', 'TAW 5.24743/79') carry an null allele at the Glu-A1 locus (Glu-A1 allele c) on chromosome arm 1AL, whereas just the 1A-1R translocation cv 'Amigo' possesses the Glu-A1 allele b for HMW glutenin subunit 2* on its chromosome arm 1AL (Table 3). Thus, a further possibility exists to identify the 1AL-1RS chromosome of 'Amigo' that is independent of the introduction of chromosome arm 1RS, but is based on the recognization of the chromosome arm 1AL of 'Amigo'. Consequently, here in the progenies of our four F_1 populations the appearance of Glu-A1 subunit 2* should be a label for the 1A-1R chromosome, while the null allele at the Glu-A1 locus indicates the presence of a normal chromosome 1A provided that a crossing-over has not taken place.

In crosses of 'Amigo', whose normal 1B chromosome carries allele c for glutenin subunits 7 and 9 on its Glu-B1 locus, with 'Ikarus' or '5.24743/79', which involve 1BL-1RS chromosomes carrying Glu-B1 alleles d and i for glutenin subunits 6+8 and 17+18, respectively, on their 1BL arms (Table 3), progenies could be checked for the absence or presence of 1B-1R chromosome by means of the corresponding Glu-B1 subunits. This possibility does not exist in crosses of 'Amigo' with 'Kawkas' and 'Iris', both of which possess the same Glu-B1 alleles for the subunits 7 and 9 on the Glu-B1 locus of their 1BL-1RS chromosomes as 'Amigo' does on its 1BL-1BS chromosome.

The 1D-coded glutenin subunits are inherited independently of the 1A-1R and the 1B-1R translocation, but because of their special importance for wheat quality they are mentioned here (Table 2, 3; Fig. 2).

On the basis of the points mentioned above all of the dh-lines, which are derived from the crosses shown in Table 1 and which possess a 1A-1R translocation chromosome, should show glutenin patterns with a Glu-A1 subunit 2*. Table 2 shows that this expectation is realized for the 9 dh-lines with a single 1A-1R translocation examined for glutenin pattern (compare dh_1 351 up to dh_1 1480). In the same way Glu-A1 subunit 2* should be observed in the 18 dh-lines with a cytologically proven 1A-1R, 1B-1R double translocation. In Table 2 this is corroborated for dh_1 667, dh_1 552 and dh_1 573 originating from F_1 population E87/5, and for dh_1 532 from E87/6, dh_2 191 to dh_1 484 from E87/145 and dh 1481 from KHK7. In Fig. 2 the HMW glutenin pattern of dh_2 191 is demonstrated.

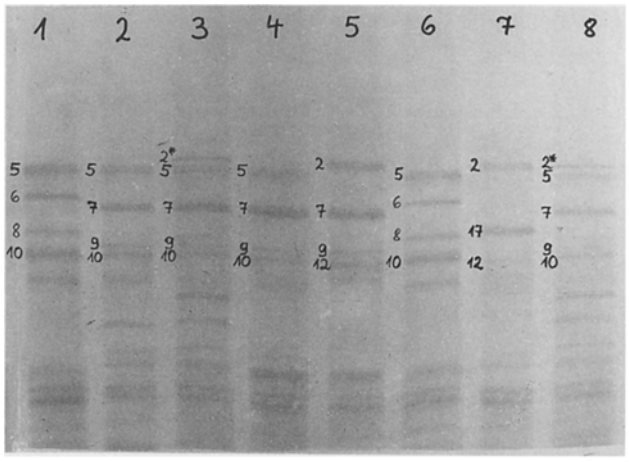

Fig. 2 HMW glutenin subunit distribution after SDS-PAGE (15% acrylamide) of reduced total seed proteins from some wheat dh-lines with different constitutions with respect to the 1RS-translocation *1* dh_1 1478 1BL-1RS, *2* dh_1 195 1BL-1RS, *3* dh_1 742 1AL-1RS, *4* dh_1 811 1BL-1RS, *5* dh_2 419 DT 1AL-1RS, 1BL-1RS, *6* dh_1 1489 1BL-1RS, *7* dh_1 457 1BL-1RS, *8* dh_2 191 DT 1AL-1RS, 1BL-1RS

The null allele on the Glu-A1 locus occurs in only 2 dh-lines (dh 1067 from E 87/5 and dh 419 from E87/6 in Table 2; for dh 419 see Fig. 2), although the cytological data and the gliadin analysis prove the presence of the 1BL-1RS and the 1AL-1RS translocation chromosomes. In this connection two facts have to be emphasized. (1) To prove that in dh 419 the subunit 2* does not exist and its absence is not merely the result of an insufficient resolution of subunits 2 and 2*, separations in gels with 7.5% acrylamide were carried out according to Payne et al. (1987). (2) The gliadin tests are mainly, and especially in such cases as discussed here, performed on the same seed as is glutenin electrophoresis; this is made possible by the analysis of half kernels.

It can therefore be concluded that for dh 1067 a crossing-over has taken place between the 1AL-1AS chromosome of 'TAW 5.24743/79' and the 1AL-1RS chromosome of 'Amigo' and that now a chromosome exists consisting of the 1RS arm of 'Amigo' and the 1AL arm of 'TAW 5.24743/79' instead of the 1RS arm and the 1AL arm of 'Amigo'. In dh-line 419 an analogous event has to have happened between the 1AL-1RS chromosome of 'Amigo' and the 1AL-1AS chromosome of 'Iris' since a 1AL-1RS chromosome composed of an 'Amigo'-1RS arm and an 'Iris'-1AL is present.

Our results with respect to the Glu-B1 subunits of the dh-lines (Table 2) meet the theoretical expectations discussed above. All of the lines from populations E87/6 and

E87/145, involving both parents with subunits 7+9, also show Glu-B1 subunits 7+9, independently of the presence of the 1BL-1BS (e.g. dh_1 887, dh_1 348 and dh_1 742) or 1BL-1RS chromosome (e.g. dh_1 811 and 446). In contrary, in crosses in which the Glu-1B subunits of the parents differ, the progenies with normal 1B chromosome always exhibit Glu-B1 subunits 7+9 that originate from the 1BL arm of 'Amigo' (compare dh_1-line 1503 without any translocation from KHK7 or for some 1A-1R translocation lines, such as dh_1 351, dh_1 390, dh_1 892 from E87/5 and dh_1 1480 from KHK7), whereas the progenies with a 1B-1R chromosome reveal either subunits 6+8 or 17+18 according to the parent from which they are derived. In this way the 1B-1R single translocation lines dh_1 1478 and 1489 as well as the 1A-1R, 1B-1R double translocation line dh 1481, all descended from F_1 population KHK7, show the same Glu-B1 subunits 6+8 as the 1B-1R translocation parent 'Ikarus' (Table 2, 3). In an analogous manner Glu-B1 subunits 17+18 appear in dh_1 457, dh_1 494 or dh_1 917 (lines with a single 1B-1R translocation) and in dh 1067, dh_1 667, dh_1 552 or dh_1 573 (lines with a 1A-1R, 1B-1R double translocation) which are all originate from E87/5 and therefore possess the 1B-1R chromosome of 'TAW 5.24743/79' (which carries the Glu-B1 locus coding for subunits 17+18). In Fig. 2 the HMW glutenin patterns of dh-lines 742, 811, 1478, 1489 and 457 are shown.

Only dh_1 195, which also descends from this cross and has a 1B-1R chromosome according to cytological and biochemical data (i.e. peroxidase zymogram type B, 1B-1R typical gliadin pattern upon SDS electrophoresis), show Glu-B1 subunits 7+9 (Table 2, Fig. 2) which does not agree with theoretical expectations. A possible explanation for this deviation could be a 1B-1R chromosome consisting of the 1RS arm of 'TAW 5.24743/79' and the 1BL arm of 'Amigo' instead of that of 'TAW 5.24743/79'. This could be a hint of the occurrence of a crossing-over between the 1BL-1RS and the 1BL-1BS chromosomes during meiosis.

Possible applicable contribution

In summary, our results have revealed the possibility of using the SDS-PAGE patterns of alcohol-soluble seed proteins for estimating the doubled haploid lines from crosses between the 1A-1R and 1B-1R translocation wheats with respect to their 1R-translocation chromosome constitution. 1A-1R, 1B-1R double translocation wheats can be detected by the absence of 1AS-coded and 1BS-coded wheat gliadins and especially by the presence of a doublet of rye proteins consisting of the 'Amigo'-typical and 'Kawkas'-typical 1RS-coded band. The use of these differences in gliadin patterns as a marker for the pre-selection of microspore-derived wheat doubled haploids with the 1A-1R, 1B-R double translocation can considerably reduce the quantity of cytological analysis necessary for ultimate proof of the desired double translocation. As discussed above, endosperm protein analysis has revealed very little evidence of instability in the 1A-1R, 1B-1R double translocation. Even the tests on nearly 100 kernels in the dh_2-generation of the doubled translocation line 1481, which originates from the corresponding anther culture regenerate plant by two self-pollination steps, showed a high level of uniformity in gliadin pattern. Because of the relatively good genetic stability of the double translocation, there should be no obstacle to using double translocation lines in the breeding process. This is highly recommendable by reason of the favourable estimation of these lines with respect to resistance against leaf diseases (Böhme 1990).

Concerning their HMW-glutenin composition the 1A-1R, 1B-1R double translocation lines were most estimated to be relatively positive (Table 2). Because of the fundamental influence of HMW glutenin subunits on the elastic properties of dough (e.g. Burnouf and Bouriquet 1980; Payne 1986; Odenbach and Mahgoub 1987; Bushuk 1989), sedimentation tests should be taken into consideration. Eventually, lines will be found with a good breadmaking quality despite the presence of the two rye translocation chromosomes. This possibility is important because the 1B-1R translocation is often associated with diminished wheat end-use quality (Zeller et al. 1982; Moonen and Zeven 1984; Payne et al. 1987; Dhaliwal et al. 1988, 1990; Rogers et al. 1989). However, no general conclusions should be drawn regarding the quality of the 1B-1R forms as certain background genetic effects may help to alleviate many of deleterious characteristics of the 1B-1R translocation; for instance, there exist German 1B-1R translocation cultivars ('Disponent', 'Herzog' and 'Olymp') with good breadmaking properties (Odenbach and Mahgoub 1987), and in the USA a few 1B-1R translocation lines (N86L238, N86L250) with the best overall baking quality and highest Glu-1 scores have been identified (Graybosch et al. 1990). According to Pena et al. (1990) the dough stickiness of 1B-1R translocation wheats might be attributable to a large extent to high-speed mixing conditions in the modern-day breadmaking process and not exclusively to the introduction of 1RS.

Our analyses of HMW glutenin patterns have enabled us to increase our knowledge of the genetic constitution of the double translocation forms because they provide information on the long arms of chromosome 1AL-1RS and 1BL-1RS. In most cases the observed glutenin subunits meet the theoretical expectations and thus support the conclusions reached with respect to the genetic constitution of the tested material by means of cytology, peroxidases and gliadins. In only 2 of the 18 dh-lines with a 1A-1R, 1B-1R double translocation (dh 1067, dh 419 in Table 2) was the null allele c instead of the

expected allele b found at the Glu-A1 locus of the 1AL-1RS chromosome. Therefore, evidence of presumable crossing-over events between the 1AL-1RS chromosome and normal 1AL-1AS chromosomes during the meiosis of F_1 plants before the anthers were removed for haploid production should be found. The observed exchange of the Glu-A1 allele, which codes for the HMW glutenin subunit 2*, by the Glu-A1 null allele is an undesirable event, because the lost subunit 2* is believed to be correlated with a good baking quality (e.g. Payne 1986; Odenbach and Mahgoub 1987). Similarly, in 1 of the 10 tested 1BL-1RS single translocation lines (dh 195 in Table 2) evidence based on HMW glutenin subunits suggests that a 1BL-1RS chromosome exists that possesses the long arm of 'Amigo' with the Glu-B1 allele c coding for subunits 7 and 9 instead of the expected subunits 17 and 18 translated by the Glu-B1 allele i of the 1BL-1RS translocation chromosome of 'TAW 5.24743/79'. However, this crossing-over between the normal 1BL-1BS chromosome of 'Amigo' and the 1BL-1RS chromosome of 'TAW 5.24743/79' has only a theoretical meaning.

These hitherto described results regarding detected cross-over events are promising for searching out further events that are of greater importance. Thus, for instance, it might be that during meiosis not only would the 1A-1R chromosome pair with the 1A chromosome, and the 1B-1R chromosome with the 1B chromosome, but also that the 1A-1R chromosome would come into contact with the 1B-1R chromosome due to the probable formation of quadrivalents between the four chromosomes with a 1RS chromosome arm. In this way crossing-over could also happen between 1A-1R and 1B-1R chromosomes, and thereby "new" 1B-1R chromosomes, including the short arm of 'Amigo' instead of the 1RS arm of 'Kawkas' or of the other 1B-1R translocation forms, could arise. "New" 1A-1R chromosomes could also be formed that possess the short arm 1RS of 'Kawkas' or the other 'Petkus' rye-derived 1B-1R translocation wheats instead of the 1RS arm of 'Amigo'.

Both imaginable "new" translocation chromosomes might bring along interesting gains. Thus, the introduction of the short arm 1RS from a 'Petkus' rye-derived 1B-1R translocation wheat into the 1A-1R translocation chromosome could possibly be accompanied by taking over the significant yield advantage discussed for 1B-1R translocation wheats arising from an unkown gene complex on the short arm of rye chromosome 1RS (Gustafson 1988; also see the results in Villareal et al. 1991 and the discussion in Lukaszewski 1990). On the other hand, the transfer of the short arm 1RS from 'Amigo' into the 1B-1R translocation could be very advantageous: the 'Insave' rye-derived 1RS arm of 'Amigo' carries effective resistance genes against mildew and greenbug (Lowry et al. 1984; Heun et al. 1990), while the 'Petkus' rye-derived mildew resistance gene of 1B-1R translocation wheats Pm8 has already been overcome in Europe (Zeller and Fuchs 1983; Friebe et al. 1989; Lukaszewski 1990; Lutz et al. 1992).

We have ascertained that such crossing-over events between 1A-1R and 1B-1R translocation chromosome had happened in the dh-material of the four crosses presented here. However, they are not described here, as they are already published in Müller et al. (1992).

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References

Berzonsky WA, Clement RL, Lafever HN (1991) Identification of 'Amigo' and 'Kawkas' translocations in Ohio soft red wheats (*Triticum aestivum* L.). Theor Appl Genet 81:629–634

Böhme T (1990) Nutzung der Antherenkultur für die Erzeugung von 1A-1R, 1B-1R-Weizen-Roggen-Doppeltranslokationslinien und deren cytologische Charakterisierung. Mitteilungen Gesellsch Pflanzenbauwissensch, 34 Jahrestagung, Bonn, pp 143–146

Böhme T, Müller G, Vahl U (1991) Zur Einlagerung der 1A-1R-Weizen-Roggen-Resistenz in die Winterweizensorte 'Ikarus'. Vortr Pflanzenzuecht 19:284–286

Burnouf T, Bouriquet R (1980) Glutenin subunits of genetically related European hexaploid wheat cultivars. Their relation to bread-making quality. Theor Appl Genet 58:107–111

Bushuk W (1989) Glutenin-Struktur und Einfluß des Glutenins auf die Backqualität. Getreide Mehl Brot 9:260–263

Dhaliwal AS, Mares DJ, Marshall DR, Skerritt HJ (1988) Protein composition and pentosan content in relation to dough stickiness of 1B/1R translocation wheats. Cereal Chem 65:143–149

Dhaliwal AS, Mares DJ, Marshall DJ (1990) Measurement of dough surface stickiness associated with 1B/1R chromosome translocation in bread wheats. J Cereal Sci 12:165–167

Friebe B, Heun M, Bushuk W (1989) Cytological characterization, powdery mildew resistance and storage protein composition of tetraploid and hexaploid 1BL-1RS wheat rye translocation lines. Theor Appl Genet 78:425–432

Graybosch RA, Peterson CJ, Hansen LE, Mattern PJ (1990) Relationship between protein solubility characteristics, 1BL-1RS, high-molecular weight glutenin composition, and end-use quality in winter wheat germ plasm. Cereal Chem 67:342–349

Gustafson JP (1988) Evaluation of a 1R (1D) substitution in wheat. In: Miller TE, Koebner MD (eds); Proc 7 Int Wheat Genet Symp. Cambridge, pp 193–196

Heun M, Friebe B, Bushuk W (1990) Chromosomal location of the powdery mildew resistance gene of 'Amigo' wheat. Phytopathol 80:1129–1133

Hollenhorst MM, Joppa LR (1983) Chromosomal location of genes for resistance to greenbug in 'Lago' and 'Amigo' wheats. Crop Sci 23:91–93

Koebner RMD, Shepherd KW (1986) Controlled introgression to wheat of genes from rye chromosome arm 1RS by induction of allosyndesis. Theor Appl Genet 73:197–208

Laemmli UK (1970) Cleavage of structural proteins during the assembly of the head of bacteriophage T4. Nature 227:680–685

Lookhart GL, Graybosch R, Peterson J, Lukaszewski A (1991) Identification of wheat lines containing the 1BL/1RS translocation by high-performance liquid chromatography. Cereal Chem 68:312–316

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

Lukaszewski AJ (1990) Frequency of 1RS.1AL and 1RS.1BL translocations in United States wheats. Crop Sci 30:1151–1153

Lutz J, Limpert E, Bartos P, Zeller FJ (1992) Identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L.) I. Czechoslovakian cultivars. Plant Breed 108:33–39

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

Mettin D, Blüthner WD, Schlegel G (1973) Additional evidence on spontaneous 1B/1R wheat rye substitutions and translocations. In: Sears ER, Sears LMS (eds) Proc 4 Int Wheat Genet Symp. University of Missouri, Columbia, Mo., pp 179–184

Moonen JHE, Zeven AC (1984) SDS PAGE of the high-molecular-weight subunits of wheat glutenin and the characterization of 1R(1B) substitution and 1BL/1RS translocation lines. Euphytica 33:3–8

Müller G, Vahl U (1986) Vergleich elektrophoretischer Peroxydasemuster von 1A-1R- und 1B-1R-Weizen-Roggen-Translokationsformen. Biochem Physiol Pflanzen 181:425–429

Müller G, Borschel H, Vahl U, Wiberg A, Härtel H, Damisch W (1989a) Die Nutzung der Antherenkulturmethode im Zuchtprozess von Winterweizen I. Zur Androgenesefähigkeit von 1B-1R-Weizen-Translokationsformen. Plant Breed 102:196–207

Müller G, Vahl U, Wiberg A (1989b) Die Nutzung der Antherenkulturmethode im Zuchtprozeß von Winterweizen II. Die Bereitstellung neuer Winterweizen-dh-Linien mit 1AL-1RS-Translokation. Plant Breed 103:81–87

Müller G, Böhme T, Borschel H, Vahl U, Wiberg A (1990) Die Nutzung der Antherenkulturmethode im Zuchtprozeß von Winterweizen III. Zur Antherenkultureignung von F1-Populationen mit den beiden heterozygoten Chromosomenpaaren 1AL-1AS/1AL-1RS und 1BL-1BS/1BL-1RS. Plant Breed 104:272–280

Müller G, Vahl U, Böhme T, Wiberg A (1992) Die 1AL-1RS-Weizen-Roggen-Translokation der "Neuen Welt" als ein neuer Genpool für mitteleuropäische Weizen. Vortr Pflanzenzuecht 22:323–324

Odenbach W, Mahgoub E (1987) Beziehungen zwischen der Backqualität und dem Vorkommen der Gene für die hochmolekularen Untereinheiten des Glutenins bei den deutschen Winter- und Sommerweizensorten. Getreide Mehl Brot 41:195–198

Payne PI (1986) Varietal improvement in the bread-making quality of wheat: contributions from biochemistry and genetics, and future prospects from molecular biology. In: BCPC Mono No 34: Biotechnology and Crop Improvement and Protection, pp 69–81

Payne PI, Lawrence GJ (1983) Catalogue of alleles for the complex gene loci, Glu-A1, Glu-B1, and Glu-D1 which code for high-molecular-weight subunits of glutenin in hexaploid wheat. Cereal Res Commun 11:29–35

Payne PI, Law CN, Mudd EE (1980) Control by homoeologous group 1 chromosomes of the high-molecular-weight subunits of glutenin, a major protein of wheat endosperm. Theor Appl Genet 58:113–120

Payne PI, Nightingale MA, Krattiger AF, Holt LM (1987) The relationship between HMW glutenin subunit composition and the bread-making quality of British-grown wheat varieties. J Sci Food Agric 40:51–56

Pena RJ, Amaya A, Rajaram S, Mujeeb-Kazi A (1990) Variation in quality characteristics associated with some spring 1B/1R translocation wheats. J Cereal Sci 12:105–112

Petrovich S, Dera AR, Gustafson JP (1988) Rye chromatin variation in Yugoslavian wheats. Plant Breed 100:83–87

Rajaram S, Mann CE, Ortiz-Ferrara G, Mujeeb-Kazi A (1983) Adaption, stability and high yield potential of certain 1B/1R CIMMYT wheats. In: Sakamoto S (ed) Proc 6 Int Wheat Genet Symp. Maruzen, Kyoto, pp 613–621

Rogers WJ, Payne PI, Harinder K (1989) The HMW glutenin subunits and gliadin compositions of German-grown wheat varieties and their relationship with breadmaking quality. Plant Breed 103:89–100

Sebesta EE, Wood EA jr (1978) Transfer of greenbug resistance from rye to wheat with X-rays. Agron Abstr 61–62

Singh NK, Shepherd KW (1988) Linkage mapping of genes controlling endosperm storage proteins in wheat 2. Genes on the long arms of group 1 chromosomes. Theor Appl Genet 75:642–650

Smith EL, Sharma RC, Merkle OG, Sebesta EE, Burton RL, Webster JA, Hunger RM, Abbott DC, Carver BF, Morgan GH (1989) Registration of Century wheat. Crop Sci 29:1093–1094

Vahl U, Müller G (1984) Elektrophoretisch getrennte Primärblatt-Peroxydasen als biochemische Marker in Winterweizenjungpflanzen. Biochem Physiol Pflanz 179:391–402

Vahl U, Müller G (1986) Nutzung elektrophoretisch getrennter Peroxydasen im Zuchtprozess von Winterweizen. Arch Zuechtungsforsch 16:1–10

Villareal RL, Rajaram S, Mujeeb-Kazi A, Del Toro (1991) The effect of chromosome 1B/1R translocation on the yield potential of certain spring wheats (*Triticum aestivum* L.). Plant Breed 106:77–81

Zeller FJ (1973) 1B/1R wheat-rye chromosome substitutions and translocations. In: Sears ER, Sears LMS (eds) Proc 4 Int Wheat Genet Symp. University of Missouri, Columbia, Mo., pp 209–221

Zeller FJ, Fuchs E (1983) Cytologie und Krankheitsresistenz einer 1A/1R- und mehrerer 1B/1R-Weizen-RoggenTranslokationssorten. Plant Breed 90:285–296

Zeller FJ, Günzel G, Fischbeck G, Gerstenkorn P, Weipert D (1982) Veraenderungen der Backeigenschaften des Weizens durch die Weizen-Roggen-Chromosomentranslokation 1B/1R. Getreide Mehl Brot 36:141–143