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1B/1R WHEAT-RYE CHROMOSOME SUBSTITUTIONS AND TRANSLOCATIONS

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SUMMARY

By means of crosses with normal wheat cultivars, several Chinese Spring monosomic lines, and the wheat-rye chromosome 1B/1R substitution lines Zorba, Salzmünde 14/44 and Weique 'Substitution', it was shown that several derivatives of Zorba have 20 wheat-chromosome pairs and an interchanged pair involving segments of wheat-chromosome 1B and rye-chromosome 1R (V). The cultivars Kavkaz and Aurora also have 1B/1R translocations. Orlando, Neuzucht, Riebesel 47/51, Wentzel, and Weihenstephan 1007/53 are 1B/1R substitution lines. Salmon has a translocation chromosome comprised of a large segment of wheat chromosome 1B and a small segment of rye chromosome 1R.

Georg KATTERMANN (1937) was the first to report a wheat-rye substitution, in which a wheat chromosome was replaced by a chromosome of rye, *Secale cereale*. Since that time a number of wheat-rye chromosome substitutions have been described by several authors. RILEY (1965) was able to substitute rye chromosome II (now designated as 6R) for all three wheat chromosomes of homoeologous group 6. SEARS (1968; personal communication) demonstrated by means of appropriate chromosome substitutions that rye chromosome III (now referred to as 2R) is genetically related to wheat chromosomes 2A, 2B and 2D. In these cases a single rye chromosome substitutes specifically for the three chromosomes of one homoeologous group in wheat.

Rye chromosomes 3R and 5R are both apparently able to substitute for wheat chromosomes of two homoeologous groups. It has been found by LEE *et al.* (1969) and GUPTA (1969) that rye chromosome 3R (VI) shows some homoeology with the group-1 chromosomes as well as with two chromosomes of homoeologous group 3. Rye chromosome 5R (I) substitutes well for at least two chromosomes of homoeologous group 5 (O'MARA, 1946; BIELIG and DRISCOLL, 1970) and for at least one chromosome of group 4, namely 4A (ZELLER and BAIER, 1973). Thus, to date, chromosomes 2R, 3R, 5R and 6R have been assigned to homoeologous wheat groups.

Also several wheat-rye translocation lines have been isolated. DRISCOLL and SEARS (1965) and SEARS (1967) produced several lines in which a translocation had been induced between a segment of the hairy-neck chromosome of rye (5R) and different wheat chromosome segments. DRISCOLL and ANDERSON (1967) found, in Transec, a translocation involving parts of wheat chromosome 4A and rye chromosome 2R carrying

[1]From a work in partial fulfillment of the requirements to obtain the 'Venia legendi' at the Technical University of Munich.

resistance to powdery mildew (*Erysiphe graminis tritici* March) and leaf rust (*Puccinia recondita* Rob. ex Desm.).

The present paper deals with the identification of several wheat-rye substitutions and translocations, in which either a complete chromosome 1B of wheat or a segment of it was replaced by a complete rye chromosome V (designated by RILEY and MACER, 1966) or a part of it.

ZORBA AND ITS DERIVATIVES

ZELLER (1969) observed only two satellited chromosomes instead of four in the somatic cells of root tips in the cultivar Zorba. Chromosomes 1B and 6B of common wheat are satellited. Studies of meiosis in monosomic F_1 plants from crosses between all 21 Chinese Spring monosomics and Zorba enabled SASTROSUMARJO and ZELLER (1970) to show that wheat chromosome 1B of Zorba was replaced by an alien chromosome. Since Zorba is a descendant of a hybrid between *Triticale* Kattermann and several *Triticum aestivum* cultivars (ZELLER 1969), it appeared reasonable to assume that the alien chromosome in Zorba was derived from rye. ZELLER and FISCHBECK (1971) studied crosses of Zorba with six wheat-rye chromosome-addition lines of Holdfast-King II and found that, in Zorba, wheat chromosome 1B was replaced by rye chromosome V. Due to the capacity of rye chromosome V to substitute for wheat chromosome 1B and the genetic relationship between this rye chromosome and wheat chromosomes of homoeologous group 1 (SHEPHERD 1968, 1973; SHEPHERD and JENNINGS, 1971), the designation 1R is proposed for rye chromosome V. The alien chromosome in Zorba is also identical to rye chromosome E of Sears' Chinese-Imperial wheat-rye addition lines (ZELLER, unpub.)

Zorba was bred in the Bayerische Landesanstalt für Bodenkultur und Pflanzenbau at Weihenstephan. It combines high resistance to rust diseases and moderate resistance to powdery mildew. It is susceptible, however, to eyespot (*Cercosporella herpotrichoides* Fron).

Due to its excellent rust resistance, Zorba was used as a crossing parent in several breeding programs at Weihenstephan. One of the most promising breeding strains in Benno, developed from the cross Zorba x Carsten VIII. Benno and all other derivatives of Zorba used in this investigation have only two SAT-chromosomes, whereas the karyotypically normal wheat varieties Chinese Spring, Kolibri, Carsten VIII and Caribo possess four satellited chromosomes.

In order to analyze its chromosome constitution, Benno was crossed with the wheat varieties Caribo and Zorba. In the F_1 hybrids (Table 1) there was good pairing in most pollen mother cells (PMC's) of the hybrids of Benno with Caribo as well as with Zorba. These results make it possible to conclude that Benno possesses a karyotype containing 20 pairs of wheat chromosomes and one pair of a wheat-rye translocation 1B/1R. Cells of Benno x Caribo with 21 bivalents had at most 20 ring bivalents and one heteromorphic rod bivalent comprised of the complete wheat chromosome 1B plus the interchanged chromosome 1B/1R in the hybrid Benno x Zorba.

The wheat strains Feldkrone [Zorba x (Heine VII x Rieti x Taca^2)], Hamlet (Zorba x Jubilar), Linos (Zorba x Jubilar) and Perseus (Zorba x Tenor) were also included in the crossing program in order to find out their chromosome constitution. In addition two more strains were chosen, since their karyotype and reaction to leaf diseases were similar to Zorba. These were Odilo (454/52 x Robert) and Urban (454/52 x Gernot), which were kindly supplied by the breeding station Lang-Doerfler. Strain 454/52 is a hybrid between TC 181 (Tassilo x Carsten V) and *Triticale* Kattermann.

Table 1. Chromosome pairing in hybrids of Benno, Feldkrone, Hamlet, Linos, Odilo, Perseus and Urban with the euploid wheats Caribo, Carsten VIII and Kolibri and with the 1B/1R substitution lines Zorba, Salzmünde 14/44, Weihenstephan 1007/53 and Weique 'Substitution'

F_1 hybrids	No. plts	21"	20" +2'	19" +4'	19" +1'v	19" +1''' +1'	18" +6'	18" +1v'	18" +1'v +2'	17" +2'v	Other
Benno x Caribo	4	63	18	-	19	3	-	-	2	2	2[1]
Benno x Zorba	4	208	84	8	19	1	-	-	11	-	-
Feldkrone x Kolibri	5	72	15	4	39	-	1	3	2	1	-
Feldkrone x Zorba	3	75	19	1	9	-	-	-	6	1	-
Feldkrone x Salzm. 14/44	4	92	36	3	31	-	-	1	2	1	2[2]
Feldkrone x Weique 'Sub.'	6	270	50	5	57	1	-	-	11	2	-
Hamlet x Caribo	5	332	38	5	32	2	-	-	6	-	-
Hamlet x Carsten VIII	2	72	7	3	1	-	-	-	-	-	-
Hamlet x Zorba	8	345	109	11	2	-	-	-	-	-	-
Linos x Caribo	3	71	17	3	8	-	1	-	2	-	-
Linos x Carsten VIII	2	20	8	-	2	-	-	-	1	-	-
Linos x Zorba	4	131	34	8	5	-	-	-	-	-	-
Linos x Salzm. 14/44	2	127	43	3	8	-	-	-	3	-	-
Odilo x Carsten VIII	4	149	13	-	36	-	-	-	-	-	1[3]
Odilo x Zorba	3	65	7	-	22	-	-	-	9	-	-
Odilo x Salzm. 14/44	2	25	6	2	1	-	-	-	4	-	-
Odilo x W 1007/53	3	88	16	2	9	-	-	-	-	-	-
Perseus x Caribo	5	68	9	3	11	-	-	-	1	1	1[4]
Perseus x Zorba	3	99	25	4	-	-	-	-	3	-	-
Perseus x Salzm. 14/44	6	154	31	3	2	-	-	-	-	-	-
Perseus x Weique 'Sub.'	1	13	5	-	2	-	-	-	-	-	-
Urban x Caribo	4	99	18	1	16	-	-	2	4	1	-
Urban x Zorba	2	15	22	2	-	-	-	-	-	-	-

[1] 17" + 1'v + 1''' + 1' and 17" + 1'v + 4'

[2] 17" + 1v' + 2' and 15" + 1v + 1'v + 3'

[3] 17" + 1'v + 1''' + 1'

[4] 16" + 1v' + 1'v

The pairing between these strains and several normal wheat cultivars as well as cytologically already identified 1B/1R wheat-rye chromosome substitution lines is summarized in Table 1. PMC's with chromosomes forming 21 bivalents or bivalents with multivalents were most frequently observed. Usually at least one heteromorphic rod bivalent was found in the metaphase plates of the F_1 hybrids. This indicates that Feldkrone, Hamlet, Linos, Odilo, Perseus and Urban possess 1B/1R wheat-rye chromosome translocations.

Figure 1 illustrates the typical pairing in an F_1 hybrid between a 1B/1R translocation (Feldkrone) and a 1B/1R substitution (Weique 'Substitution'). Nineteen bivalents and one quadrivalent are formed. The heteromorphic rod bivalent involves the complete rye chromosome 1R of Weique 'Substitution' (see later) and the interchanged chromosome 1B/1R of Feldkrone.

SALZMÜNDE 14/44 AND ITS DERIVATIVES

Salzmünde 14/44 was developed independently of Zorba by Georg Riebesel and is believed to have originated from the cross Criewener 104 x Petkus rye. Salzmünde 14/44 has remarkable resistance to rust diseases and powdery mildew and was released commercially under the name Salzmünder Bartweizen from 1957-1961 in East Germany. The variety has 40 wheat chromosomes plus one pair of rye chromosomes 1R (ZELLER, 1972), and the karyotype of root-tip mitoses has only two SAT-chromosomes.

At the Hohenthurm breeding station (East Germany) the wheat strain Salzmünde 26/47 has been widely used as crossing parent (LEIN, personal communication). This strain most probably was developed by Riebesel, too, and has been used for the hybridization of the commercial variety Orlando. The disease resistance of Orlando is very similar to Salzmünde 14/44.

Orlando was crossed with Caribo, Zorba and Salzmünde 14/44. In the Orlando x Caribo hybrids the configuration 20"+2' occurred most frequently, and in the crosses Orlando x Zorba and Orlando x Salzmünde 14/44, 21" were usually formed (Table 2). This leads to the conclusion that Orlando is a substitution line, in which wheat-chromosome 1B was replaced by rye-chromosome 1R (see METTIN *et al.*, 1973).

Another strain, Neuzucht (Newbred), is probably identical to Salzmünde 14/44; Crosses between Neuzucht and Caribo, Zorba, Salzmünde 14/44 and Weique 'Substitution' (Table 2) reveal that this strain is similar to Salzmünde 14/44 and Zorba in possessing a complete 1B/1R chromosome substitution. The presence of usually 21 bivalents and the absence of quadrivalents and other multivalents in Neuzucht x Salzmünde 14/44 (Table 2) support the assumption that both varieties are identical.

Neuzucht has been used in the parentage of the cultivars Kavkaz and Aurora (LUKYANENKO, personal communication). Both Kavkaz and Aurora originated from the cross (Bezostaya 4 x Neuzucht) F_5 x Bezostaya 1 (VORONKOVA, personal communication).

Pairing in PMC's was analyzed in 41 chromosome hybrids between several Chinese Spring monosomic lines (kindly supplied by Dr. E. R. SEARS) and Kavkaz and Aurora, respectively (Table 3). The commonest chromosome configuration was 20"+1'. In crosses of Kavkaz and Aurora with Caribo, Zorba, Salzmünde 14/44 and Weique 'Substitution', the

Table 2. Chromosome pairing in hybrids of Orlando, Neuzucht, Kavkaz and Aurora with Caribo (normal), Zorba, Salzmünde 14/44 and Weique 'Substitution' (1B/1R substitution lines).

F_1 hybrids	No. plts.	21"	20" +2'	19" +4'	19" +1'V	19" +1"' +1'	18" +6'	18" +1'V +2'	17" +1'V +4'	16" +1V' +4'	Other
Orlando x Caribo	7	-	141	15	-	-	-	44	-	-	2[1]
Orlando x Zorba	5	94	27	1	-	-	-	-	-	-	-
Orlando x Salzm. 14/44	2	366	52	-	8	-	-	-	-	-	-
Neuzucht x Caribo	5	-	134	61	-	-	9	23	14	3	2[2]
Neuzucht x Zorba	1	54	9	1	1	2	-	-	-	-	1[3]
Neuzucht x Salzm. 14/44	1	90	33	2	-	-	-	-	-	-	-
Neuzucht x Weique 'Sub.'	2	95	11	-	-	-	-	-	-	-	-
Kavkaz x Caribo	1	31	4	1	7	-	-	5	-	-	-
Kavkaz x Zorba	4	63	32	2	1	-	-	7	-	-	-
Kavkaz x Weique 'Sub.'	2	154	32	2	11	-	3	-	-	-	-
Aurora x Zorba	4	256	67	-	16	-	-	-	-	-	-
Aurora x Salzm. 14/44	4	142	64	7	12	2	-	2	-	-	-

[1]17" + 1V' + 2' and 16" + 2'V + 2'.

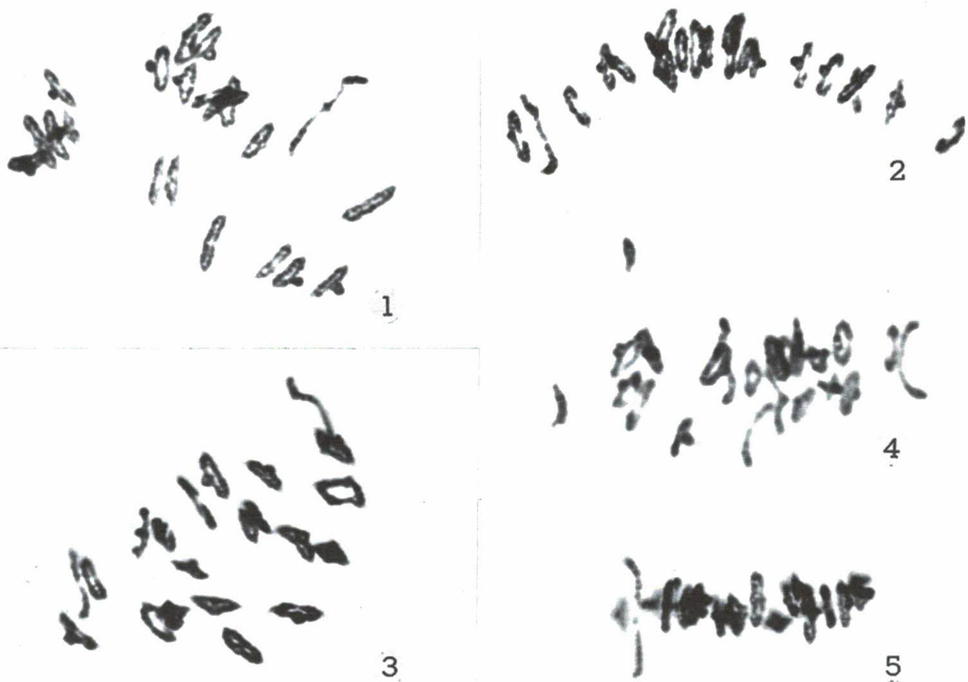
[2]16" + 2'V + 2' and 16" + 1'V + 6'.

[3]17" + 2'V.

Table 3. Chromosome pairing in monosomic F_1 plants of several Chinese Spring monosomics x Kavkaz and Aurora

F_1 hybrids	No. of plants	20"+1'	19"+3'	18"+5'	18"+1'V +1'	18"+1"' +2'	17"+7'	17"+1'V +3'
Mono-7A x Kavkaz	3	83	17	-	-	-	-	1
Mono-2B x Kavkaz	5	104	26	7	8	1	-	-
Mono-5B x Kavkaz	4	84	11	3	3	-	-	-
Mono-1D x Kavkaz	2	48	18	2	5	-	-	1
Mono-4D x Kavkaz	2	51	11	2	5	-	-	-
Mono-1B x Aurora	2	69	20	1	7	-	1	1
Mono-7D x Aurora	4	78	46	5	3	-	-	-

chromosomes usually formed bivalents and multivalents, although univalents occurred at a lower frequency (Table 2). These results permit the conclusion that Kavkaz and Aurora possess an interchanged chromosome pair consisting of a wheat chromosome 1B segment and a rye chromosome 1R segment (see METTIN *et al.*, 1973). Figure 2 illustrates the pairing behavior in a hybrid between Kavkaz and Weique 'Substitution'. The chromosome pair with the interchanged chromosome of Kavkaz and the complete rye chromosome of Weique is clearly visible as a heteromorphic rod bivalent among 20 ring bivalents. Karyotype analyses of Kavkaz and Aurora again showed only two SAT-chromosomes in the somatic cells of root tips.



Figures 1 to 5. MI in PMC's of F_1 hybrids. (1) Weique 'Substitution' x Feldkrone, showing 18" (closed) +1'V+1" (heteromorphic rod consisting of rye chromosome 1R and the interchanged chromosome 1B/1R). (2) Kavkaz x Weique 'Substitution' with 20" (ring) +1" (heteromorphic rod). (3) Caribo x Wentzel, showing 18"+1'V+2' (1B and 1R). (4) Zorba x Weihenstephan 1007/53 with 21". (5) Salmon x Salzmünde 14/44, showing 20" (closed) +1" (heteromorphic rod consisting of 1R and 1B/1R).

WEIQUE, RIEBESEL 47/51 AND WENTZEL

Weique is a wheat cultivar bred by Georg Riebesel and released commercially in 1960 in West Germany. Its comprehensive resistance to stem, leaf and stripe rust is well known. WIENHUES (1965) reported that Weique is a substitution line, in which a pair of wheat chromosomes is replaced by a pair of alien chromosomes. Formerly it was believed that the alien chromosome was derived from *Agropron intermedium*, but after morphological studies of the unpaired chromosomes at meiosis in the hybrid Weique x Heine IV, WIENHUES (1965) suggested that the non-wheat chromosome might have been obtained from rye. In crosses between Weique (seed supplied by Dr. Wienhues) and the wheat-rye addition line V of Holdfast-King II as well as Zorba, Salzmünde 14/44 and several Chinese Spring monosomics, ZELLER and SASTROSUMARJO (1972) found that rye chromosome V (1R) is present in Weique in place of wheat chromosome 1B.

In crosses between Weique (seed supplied by the breeding station von Lüttichau & Riebesel) and Zorba, Salzmünde 14/44 and several Chinese Spring aneuploids, however, the alien chromosome substitution could not be confirmed. In this breeder's Weique, which represents the commercial variety, ZELLER and SASTROSUMARJO (1972) found that a translocation was present involving segments of rye chromosome 1R and wheat chromosome 1B. The formerly complete wheat chromosome 1B has lost the short satellited arm or a part of it, and the residual segment of 1B and a segment of rye chromosome 1R have been combined into a translocated chromosome (ZELLER and SASTROSUMARJO, 1972). Thus the cultivar Weique consists of two sublines: Weique 'Substitution' with a 1B/1R chromosome substitution and Weique 'Translocation' with an interchanged chromosome 1B/1R.

There are two other wheat strains, most probably developed by the breeder Riebesel, that are known under the names Riebesel 47/51 and Wentzel. R 47/51 belongs to the stripe-rust tester set of the Nederlands Graan Centrum and is resistant to all so-far-recognized physiological races of *Puccinia striiformis* (JOHNSON *et al.*, 1972). R 47/51 probably came from The Netherlands to the United States, where it was designated as P.I. 295999 in the world wheat collection of Beltsville.

Table 4. Chromosome pairing in hybrids of Riebesel 47/51 and Wentzel with the euploids Caribo, Carsten VIII and Kolibri, and the 1B/1R substitutions Zorba, Salzmünde 14/44 and Weique 'Substitution'

F_1 hybrids	No. plts.	21''	20'' +2'	19'' +4'	19'' +1'V	19'' +1''' +1'	18'' +6'	18'' +1'V +2'	17'' +1'V +4'	16'' +2'V +2'	Other
Riebesel 47/51 x Kolibri	6	-	179	7	-	-	2	41	2	-	-
Riebesel 47/51 x Zorba	10	599	32	2	41	1	-	-	-	-	1[1]
Riebesel 47/51 x Weique 'Sub.'	4	185	15	-	29	1	-	-	-	-	-
Wentzel x Caribo	8	-	320	18	-	-	-	82	2	4	2[2]
Wentzel x Carsten VIII	3	-	129	3	-	-	1	17	-	-	-
Wentzel x Zorba	1	20	3	-	2	-	-	-	-	-	-
Wentzel x Salzm. 14/44	2	109	10	-	14	-	-	-	-	-	-
Wentzel x Weique 'Sub.'	1	15	6	-	4	-	-	-	-	-	-

[1] 17'' + 2'V.

[2] 18'' + 1''' + 3' and 15'' + 2'V + 4'.

Riebesel 47/51 was crossed with Kolibri, Zorba and Weique 'Substitution' and the PMC's of the hybrids were analyzed. The data (Table 4) clearly indicate that R 47/51 represents a complete 1B/1R wheat-rye chromosome substitution.

Wentzel was supplied by the breeding station Lang-Doerfler. Chromosome configurations in crosses of Wenzel with Caribo, Carsten VIII, Zorba, Salzmünde 14/44 and Weique 'Substitution' (Table 4) reveal that this strain also is a 1B/1R substitution line. Figure 3 shows the pairing in a hybrid between Caribo and Wentzel, with 18"+ 1'V+2' being formed. The two unpaired chromosomes are wheat chromosome 1B and rye chromosome 1R, respectively.

WEIHENSTEPHAN 1007/53

Karl Wenisch of the Bayerische Landesanstalt für Bodenkultur und Pflanzenbau at Weihenstephan developed the wheat strain W 1007/53. Its resistance to mildew and rust diseases is remarkable and resembles that of Zorba. W 1007/53, however, was produced independently of Zorba, Salzmünde 14/44 and Weique from the hybrid *Triticum turgidum* ssp. *durum* var. Heines Hartweizen[2] x 4n *Secale cereale* var. Petkuser Tetraroggen.

Table 5. Chromosome pairing in monosomic F_1 plants of 16 different Chinese Spring monosomics with Weihenstephan 1007/53

Monosomic	No. plants	20" +1'	19" +3'	18" +5'	18" +1'V +1'	18" +1''' +2'	17" +7'	17" +1'V +3'	17" +1''' +4'	16" +1'V +5'	Other
1A	5	-	126	13	-	-	1	2	-	-	-
2A	4	-	140	41	-	-	-	7	-	2	-
3A[1]	5	-	169	18	-	3	-	2	-	1	-
4A	5	-	128	51	-	-	7	2	1	1	-
5A	2	-	34	1	-	-	-	1	-	-	-
6A	7	-	170	14	-	-	-	2	1	1	1[2]
7A	5	-	121	27	-	-	1	2	-	-	1[3]
1B	3	203	34	3	8	-	2	-	-	-	2[4]
2B[1]	2	-	35	7	-	2	-	-	-	-	-
3B	3	-	116	17	-	-	-	3	-	-	-
4B	1	-	33	3	-	-	-	1	-	-	-
5B	2	-	71	5	-	-	-	2	-	-	-
6B	2	-	69	25	-	-	-	-	1	-	-
7B	1	-	32	4	-	-	2	2	-	-	-
1D	3	-	41	10	-	-	-	-	-	-	-
7D	1	-	54	9	-	-	1	2	-	-	-

[1] 3A and 2B interchanged in Weihenstephan 1007/53.

[2] 15" + 2'V + 3'.

[3] 15" + 9'.

[4] Both 16" + 2'V + 1'.

The somatic chromosome count revealed that W 1007/53 has 42 chromosomes with only two SAT-chromosomes. The strain was crossed with 16 different Chinese Spring monosomics (kindly supplied by Dr. E. R. SEARS) and the chromosome behavior analyzed in PMC's of the monosomic F_1 hybrids (Table 5). Fifteen hybrids showed predominantly 19"+3', but in the critical cross, mono-1B, mainly 20"+1' were formed. From this it is evident that W 1007/53 represents an alien-chromosome substitution.

In order to identify the non-wheat chromosome, this strain was crossed with Zorba, Salzmünde 14/44 and Weique 'Substitution'. F_1 plants were characterized by 21 bivalents most commonly (Table 6). In Figure 4 a PMC of Zorba x W 1007/53 is shown with 21 bivalents. The results of the chromosome behavior listed in Table 6 indicate that in W 1007/53 wheat chromosome 1B is replaced by rye chromosome 1R.

Table 6. Chromosome pairing in hybrids of Weihenstephan 1007/53 with Caribo (euploid) and Zorba, Salzmünde 14/44 and Weique 'Substitution' (1B/1R substitutions)

Male parent	No. plants	21"	20" +2'	19" +4'	19" +1'V	18" +1'V +2'	18" +1''' +3'	17" +1V' +2'	Other
Caribo	6	-	210	20	-	49	5	2	3[1]
Zorba	3	246	19	1	16	-	-	-	-
Salzm. 14/44	4	264	45	4	6	-	-	-	1[2]
Weique 'Sub.'	4	165	17	3	10	4	-	-	-

[1] 18" + 6', 16" +1V' + 4', and 16" + 2'V + 2'.

[2] 17" + 8'.

SALMON

In 1964 TSUNEWAKI described a hexaploid wheat strain, named Salmon, that was obtained in the progeny of a hybrid between two strains of octaploid *Triticale*. From the appearance of a heteromorphic rod bivalent consisting of a satellited and a non-satellited partner in PMC's of the cross Salmon x Chinese Spring and the presence of only two SAT-chromosomes in root-tip mitoses of Salmon, TSUNEWAKI (1964) concluded that the satellited arm of one of the two wheat SAT-chromosomes in Salmon was replaced by an arm of a rye chromosome.

Table 7. Chromosome pairing in hybrids of Salmon with Zorba and Salzmünde 14/44

Male parent	No. plants	21"	20" +2'	19" +4'	19" +1'V	19" +1''' +1'	18" +6'	18" +1'V +2'	18" +1''' +3'	17" +1'V +4'	16" +2'V +2'	Other
Zorba	12	99	355	77	19	3	3	30	6	2	3	3[1]
Salzm. 14/44	4	56	303	57	11	4	-	21	11	-	-	-

[1] 17" + 2'V, 17" + 1'V + 1''' + 1', and 17" + 1''' + 5'.

Since the karyotypes of Salmon and the above-described substitution and translocation lines are very similar to each other, Zorba and Salzmünde 14/44 were crossed to Salmon (seed kindly supplied by Dr. TSUNEWAKI) and F_1 plants analyzed. As shown in Table 7, 20"+2' was observed most commonly, but 21" (Figure 5) and $19"+1'^{V}$ occurred too, though at a lower frequency. From the latter configuration it may be concluded that a segment of chromosome 1B in Salmon is combined with a small part of rye chromosome 1R which is homologous to a segment of the alien chromosomes in Zorba and Salzmünde 14/44.

LOCATION OF GENES FOR DISEASE RESISTANCE ON RYE CHROMOSOME 1R

In a comprehensive study to locate genes for disease resistance to wheat pathogens on rye chromosomes in wheat-rye addition lines (Holdfast-King II), RILEY and MACER (1966) found that rye chromosome V, now designated as 1R, carries on its short arm genetic factors conditioning resistance to powdery mildew (*Erysiphe graminis tritici*) and stripe rust (*Puccinia striiformis* Westend.). Genetic investigations of BARTOŠ and BAREŠ (1971) indicate that the cultivars Salzmünder Bartweizen and Weique have identical genes for leaf-rust (*P. recondita*) and stem-rust (*P. graminis* Pers. var. *tritici*) resistance. These two genes and a gene(s) for mildew resistance are believed to be linked (BARTOŠ and BAREŠ, 1971).

In contrast to these findings OPPITZ (personal communication) was unsuccessful in locating a gene for resistance to stem rust, race 21, in an analysis of the F_2 from monosomics derived from the cross of the 21 Chinese Spring monosomics x Weihenstephan 1007/53.

Therefore a Chinese Spring/Zorba substitution line, in which Chinese chromosome 1B was replaced by Zorba chromosome 1R after four backcrosses, was used in order to test the reaction of leaf diseases. Seedlings of Zorba, Chinese Spring and Chinese Spring 1R(1B) were inoculated with urediospores of stem rust, race 21, and leaf rust, race UN 10-14b. BARTOŠ, who made the pathological inoculations, found that race 21 and race UN 10-14b are virulent to Chinese Spring, but avirulent to Zorba and the Chinese Spring 1R(1B) substitutions.

Inoculations with *P. striiformis* were carried out by FUCHS using urediospores of the physiologic races O E 64, 32 E 128 and 36 E 132 (nomenclature after JOHNSON *et al.*, 1972). Chinese Spring was susceptible to all the races used, whereas Zorba and Chinese Spring 1R(1B) were resistant to them (FUCHS, personal communication).

From these results it is clear that rye chromosome 1R in Zorba carries linked genes for resistance to *P. graminis* f. sp. *tritici*, *P. recondita* and *P. striiformis*. It appears likely that most of the leaf-disease resistance of the above-mentioned wheat strains with alien variation transferred from rye possess these genes for resistance to stem, leaf and stripe rust. A program to allocate also the mildew resistance by means of isogenic 1R(1B) substitution lines is now being initiated.

DISCUSSION

From the results obtained some general conclusions can be deduced. The disease resistance of *Secale* chromosome 1R in the above-described wheat strains serves as a potentially useful source in wheat breeding. Salzmünder Bartweizen, Weique and Orlando, which possess the complete rye chromosome 1R, were and are being grown commercially. Kavkaz and Aurora, which have the 1B/1R translocation, are being cultivated as important varieties in eastern European countries, especially in the Soviet Union. Feldkrone, Hamlet, Linos, Odilo, Perseus, and Urban in West Germany appear to be very promising strains that will probably be released commercially in the near future. Benno is a high-yielding variety released in 1973. Weihenstephan 1007/53, which has the 1B/1R substitution, is promising in the present breeding work.

With the general confirmation of the occurrence of alien-chromosome substitution lines in wheat, interest has recently concentrated upon the nature of the relationship between the substituting alien chromosome and the replaced wheat chromosome. If a chromosome of the subtribe *Triticinae* will only substitute for those of one homoeologous group of wheat, this chromosome may be said to have *specific substituting ability* (RILEY *et al.*, 1966). By contrast, if an alien chromosome will substitute for the chromosomes of more than one homoeologous group, it may be said to have *general substituting ability* (RILEY *et al.*, 1966). From the present results it may be concluded that rye chromosome 1R shows a preferred tendency to eliminate wheat chromosome 1B in spontaneous substitutions and therefore exhibits *preferential substituting ability.*

Although there is good compensation of rye chromosome 1R for the eliminated wheat chromosome 1B, the 1B/1R translocation strains appear to be more stable than the 1B/1R substitutions and superior to them in agronomic properties as well. In order to use the 1B/1R translocation lines in breeding programs, breeders only need to select for leaf-disease resistance. This is of great advantage, since cytological work is not needed for the successful introduction of the desired segment of rye chromosome 1R into common wheat. It is even possible to incorporate this rye segment into tetraploid wheats.

It may be interesting to investigate whether the breaks of the translocations involving chromosome segments of 1B and 1R have taken place always at the same points in the mentioned wheat strains. It should be possible to locate the break points by means of marker genes on chromosomes 1B and 1R, respectively.

From the breeder's point of view it may be of interest to know whether the rye resistance of chromosome 1R in common wheat will provide a type of resistance that will not be overcome by new mildew and rust races. This question can be considered in the light of selection pressure on the pathogen and its possibilities of variation for pathogenicity. It is very likely that the selection pressure for the recombination of new genes or alleles for virulence of the pathogen will be considerably increased when the acreage of wheat varieties having the alien segment with the disease resistance is greatly extended.

It has been shown by several authors that sexual and somatic hybridization can be induced between wheat stem rust (*Puccinia graminis* f.sp. *tritici*) and rye stem rust (*P. graminis* f.sp. *secalis*) in the field and in the laboratory (JOHNSON, 1949; WATSON and LUIG, 1968; GREEN, 1971; LUIG and WATSON, 1972). Hybridization between *Erysiphe graminis* f.sp. *tritici* and *E. graminis* f.sp. *agropyri* has also been successfully conducted (HIURA, 1962, 1964; HIURA and HETA, 1969). Some of these experiments revealed that the progenies of appropriate hybrids between *formae speciales* were avirulent on common wheat (JOHNSON, 1949; HIURA, 1964; WATSON and LUIG, 1968; LUIG and WATSON, 1972). In contrast to these findings HIURA and HETA (1969) and SANGHI and LUIG (1971) observed several new physiological races from hybrids of *formae speciales* that were able to attack common-wheat varieties. From these results it can be concluded that disease resistance from related genera transferred to wheat may not involve a different type of gene action from that which is operating in *Triticum*. They also suggest that resistance of rye and *Agropyron* incorporated into wheat may be overcome by hybrids between *formae speciales* of *Puccinia graminis* and of *Erysiphe graminis*, respectively. Thus the introduction of alien genetic variation into wheat, especially disease resistance from genera of the subtribe *Triticinae*, must not be considered as a means to solve problems of disease resistance in a permanent way, but only as a complement to the already existing tools in practical wheat breeding.

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