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Identification of 'Amigo' and 'Kavkaz' translocations in Ohio soft red winter wheats (*Triticum aestivum* L.)*

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Summary. One cultivar ('GR876') and two advanced Ohio soft red winter wheat lines ('OH413' and 'OH414'), with 'Kavkaz' in their pedigrees, were examined for the presence of the 'Kavkaz,' *1RS/1BL* rye/wheat chromosome translocation. Another advanced line ('OH416'), with 'Amigo' in its pedigree, was examined for the presence of the 'Amigo,' *1RS/1AL* translocation. Only two satellited chromosomes were observed in most mitotic root-tip cells from 'GR876,' 'OH413,' and 'OH414,' compared to four in most cells from 'OH416.' Heteromorphic bivalents were observed in most PMCs from hybrids produced by crossing 'GR876,' 'OH413,' and 'OH414' as females to 'Chinese Spring.' No heteromorphic bivalents were observed in PMCs from 'OH416' × 'Chinese Spring' hybrids. When 'GR876' and the Ohio lines were hybridized with 'Chinese Spring' dimonotelosomic-*1B*, telosomic trivalents, consisting of the short- and long-arm telosomes paired with chromosome *1B*, were only observed in PMCs from 43-chromosome hybrids involving 'OH416.' The long-arm telosome paired with the translocation chromosome, while the short-arm telosome remained unpaired in all other 43-chromosome hybrids. Separation of gliadin proteins from 'GR876' and the Ohio lines by PAGE revealed that secalin bands for 'GR876,' 'OH413,' and 'OH414,' migrated similarly to the secalins for 'Kavkaz.' Bands for 'OH416,' identified as possible secalins, migrated similarly to those for 'Amigo.' Cultivar 'GR876' and advanced Ohio soft red winter wheat lines 'OH413' and 'OH414' carry the 'Kavkaz' translocation, while 'OH416' carries the 'Amigo' translocation.

Key words: Rye – Soft red winter wheat – Chromosome translocations – Telosomic analysis – Secalins

Introduction

Chromosome *1R* of rye, *Secale cereale* L., carries valuable genes for disease resistance (Riley and Macer 1966; Bartos et al. 1973; Bhalla et al. 1973) and insect resistance (Harvey and Livers 1975; Hollenhorst and Joppa 1983). Breeders have transferred these genes by selecting for resistance among progeny produced from hybrids between rye and hard or soft wheats. This has led to the production of wheat cultivars having translocations involving chromosome *1R* and the homoeologous group 1 chromosomes of wheat (Zeller and Hsam 1983). Hard winter wheat cultivar 'Amigo' has been identified as having the short arm of chromosome *1R* (*1RS*) translocated to the long arm of chromosome *1A* (*1AL*) (Zeller and Fuchs 1983). 'Kavkaz,' a hard winter wheat cultivar introduced from the USSR has a *1RS/1BL* translocation (Mettin et al. 1973; Bennett and Smith 1975). The 'Kavkaz' translocation may be identified by the presence of only two satellited chromosomes in mitotic root-tip cells (Merker 1982), because *1RS* contracts and the nucleolar organizing region fuses with its short arm in a wheat background (Merker 1973). 'Amigo' and 'Kavkaz' have been widely employed by breeders to introduce translocations into other hard or soft wheats (Zeller 1973).

Unfortunately, introducing the 'Kavkaz' translocation into hard wheats has been associated with reducing their bread-baking quality (Martin and Stewart 1986; Dhaliwal et al. 1987). However, introduction into soft

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wheats does not appear to lead to similar quality defects (Dhaliwal et al. 1988). Therefore, introducing 'Amigo' and 'Kavkaz' translocations into Ohio soft red winter wheats promises to lead to the production of disease and insect-resistant cultivars lacking the quality defects associated with their introduction into hard wheats.

As an aid to the production of such cultivars, this study was initiated to identify whether or not one cultivar and three advanced Ohio soft red winter wheats contain 'Amigo' or 'Kavkaz' translocations.

Materials and methods

Plant materials

'GR876,' the most recent Ohio soft red winter wheat cultivar to be licensed to the Agricultural Genetic Research Association (AGRA), was developed from hybridization involving 'Kavkaz' ('Hart'/'Va. 66-54-10'/'Kavkaz'/Pur. 6693'). Seed of 'GR876' for analyses was obtained from 1987 field-grown plants. Advanced Ohio soft red winter wheat lines 'OH413,' 'OH414,' and 'OH416' were developed from F_3 plant selections. 'Kavkaz' is in the pedigree of 'OH413' ('Gr876'/'Oh217') and 'OH414' ('GR876'/'OH239'ß). 'Amigo' is in the pedigree of 'OH416' ('Fillmore'/'Amigo'). Seed of 'OH413,' 'OH414,' and 'OH416,' used in analyses, was derived from 1988 field-grown plants in the F_8 generation. 'Amigo' and 'Kavkaz' wheats were employed as check cultivars. 'Veery' was employed as an additional check cultivar in the electrophoretic analyses, since it is also known to carry a *1RS/1BL* translocation (Merker 1982). Seed of these cultivars was obtained from stocks maintained at the Ohio Agricultural Research and Development Center. Seed of the rye inbred cultivar '2a' was provided by A. Lukaszewski, University of California-Riverside. Seed of the 'Imperial' *1R* addition line of 'Chinese Spring' was provided by E. R. Sears, University of Missouri-Columbia.

Cultivar 'GR876,' each Ohio line, and the 'Amigo' and 'Kavkaz' checks were used as females in hybridizations with euploid 'Chinese Spring' and 'Chinese Spring' dimonotelosomic-*1B* (seed provided by G. Kimber, University of Missouri-Columbia). Hybrids with 43 chromosomes, having the short and long arms of chromosome *1B*, were identified by root-tip counts and selected for meiotic analyses. Euploid and selected 43-chromosome hybrids, subjected to meiotic analyses, were grown in the glasshouse.

Cytological analyses

Mitotic root-tip squashes were prepared from 12–17 seedlings of the 'Amigo' and 'Kavkaz' checks, 'GR876,' and each Ohio line. Root tips were collected from seeds germinated overnight at 25 °C on moistened filter paper. Roots were treated for 4 h in an aqueous saturated solution of monobromonaphthalene containing several drops of dimethyl sulfoxide. This solution was replaced with glacial acetic acid and samples were placed in a refrigerator (2–3 °C) for at least 24 h. Squashes were prepared according to a modification of the technique described by Sallee and Kimber (1983). Satellited chromosomes were more easily identified when root tips were squashed in 1% acetic-lacmoid, prepared as described by Darlington and LaCour (1950). Satellited chromosomes were counted in 48 well-spread mitotic root-tip cells from each cultivar and line.

Smears of pollen mother cells (PMCs) of the hybrids were prepared from anthers collected from heads at the early boot stage. Anthers with metaphase PMCs were identified in temporary acetocarmine smears (Darlington and LaCour 1950) and fixed in a 3:1 95% alcohol:glacial acetic acid mixture. Fixed anthers were hydrolized in 1 *N* HCl for 12 min, stained with Feulgen (Darlington and LaCour 1950), and smeared in propionic orcein. Slides were made permanent by mounting a coverslip with Canada Balsam after passing them through a 50:50 100% tertiary butyl alcohol (TBA): glacial acetic acid mixture and two changes of 100% TBA. Meiotic observations were made for at least ten well-spread PMCs in each hybrid. Meiotic configurations were recorded following the nomenclature introduced by Kimber and Sears (1968).

Table 1. Satellited chromosome counts of mitotic root-tip cells from 'Amigo,' 'Kavkaz,' 'GR876,' 'OH413,' 'OH414,' and 'OH416'

Cultivar/ line	No. of seedlings analyzed	No. of cells observed	No. of satellited chromosomes				
			0	1	2	3	4
'Amigo'	14	48	–	2	8	13	25
'Kavkaz'	12	48	–	5	36	3	4
'GR876'	13	48	–	13	34	1	–
'OH413'	14	48	5	15	28	–	–
'OH414'	15	48	2	9	36	1	–
'OH416'	17	48	2	3	6	13	24

Electrophoretic analysis of gliadins

Gliadin proteins were extracted from crushed, single kernels with ethylene glycol, and electrophoresis was performed on polyacrylamide gel (PAGE) using a continuous acetic acid system (Clements 1988). Gliadins were stained with Coomassie Brilliant Blue G-250 in 5% sodium sulfate/2% trichloroacetic acid (Clements 1990). Nineteen single-kernel samples from each check cultivar, 'GR876,' and each Ohio line were electrophoresed.

Results

Cytological analyses

A range of zero to four satellited chromosomes was observed in root-tip cells from seedlings of the check cultivars ('Amigo' and 'Kavkaz'), 'GR876,' 'OH414,' and 'OH416' (Table 1). However, cells with only two satellited chromosomes (Fig. 1 a) predominated in the observations for 'GR876,' 'OH413,' and 'OH414,' similar to the observations for 'Kavkaz,' in which 75% of the observed cells had only two satellited chromosomes. Cells from 'OH416' mostly contained four satellited chromosomes as did those from 'Amigo,' in which 52% of the observed cells had four satellited chromosomes.

Observations of PMCs from hybrids involving 'Chinese Spring' revealed chromosomes paired as bivalents, trivalents, and quadrivalents (Table 2). The most frequent meiotic configuration observed, except in hybrids involving 'OH413,' was 21″ pairing. In addition, a bivalent consisting of a satellited chromosome and a chromo-

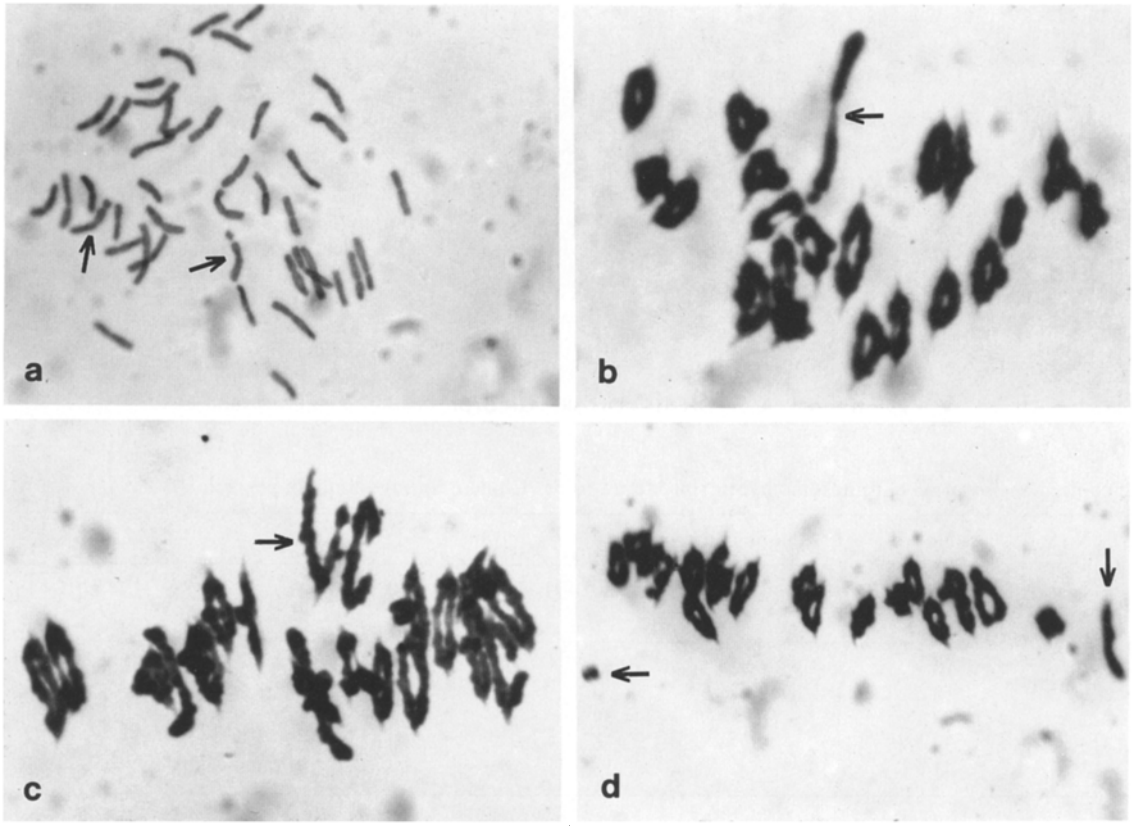

Fig. 1. **a** Mitotic root-tip chromosomes of 'OH414'. *Arrows* indicate two satellited chromosomes. **b** Metaphase I in PMC of 'OH414' × 'Chinese Spring' hybrid. *Arrow* indicates heteromorphic bivalent. **c** Metaphase I in PMC of a 43-chromosome hybrid 'OH416' × 'Chinese Spring' dimonotelosomic-*1B*. *Arrow* indicates telosomic trivalent. **d** Metaphase I in PMC of a 43-chromosome hybrid 'GR876' × 'Chinese Spring' dimonotelosomic-*1B*. *Arrows* indicate short-arm univalent and bivalent, consisting of the long-arm telosome and a translocation chromosome

Table 2. Meiotic configurations of 42-chromosome hybrids produced using 'Chinese Spring' as male parent

Female parent	No. of plants analyzed	No. of PMCs observed	Meiotic configuration[a]				
			$17''+8'-20''+2'$	$21''$	$18''+1'''+3'$	$19''+1'''+1'$	$17''+1^{IV}+4'-19''+1^{IV}$
'Amigo'	3	39	7	28	1	1	2
'Kavkaz'	3	33	13 (3)	19 (13)	–	–	1
'GR876'	4	70	7 (1)	50 (27)	–	–	13 (6)
'OH413'	4	72	39 (12)	32 (17)	–	–	1
'OH414'	2	38	6 (4)	32 (23)	–	–	–
'OH416'	4	69	17	52	–	–	–

[a] Number in parentheses indicates the number of PMCs in which one heteromorphic bivalent was also observed

some without a secondary constriction (heteromorphic bivalent, Fig. 1 b) was identified in many configurations from hybrids involving 'Kavkaz,' 'GR876,' 'OH413,' and 'OH414.' Though chromosomes of 'Amigo' and 'OH416' hybrids frequently formed bivalents, no heteromorphic bivalents were ever observed. Chromosomes from hybrids produced with 'GR876' often formed quadrivalents, suggesting that reciprocal translocations exist between this cultivar and 'Chinese Spring'.

Meiotic configurations observed for the 43-chromosome hybrids, having the short- and long-arm telosomes of chromosome *1B*, are represented in Table 3. Hybrids involving 'Amigo' were not obtained. Only in hybrids involving 'OH416' did the short and long arms pair with

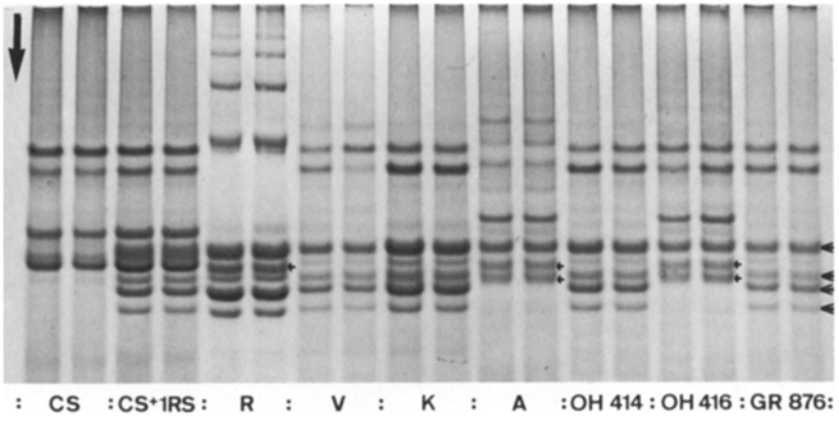

Fig. 2. Upper portion of an acid polyacrylamide gel electrophoresis (PAGE) showing the migration of gliadins extracted from two kernels of the following (*left* to *right*): 'Chinese Spring' (CS), 'Imperial *1R*' addition to 'Chinese Spring' (CS + *1R*), '2a' rye (R), 'Veery' (V), 'Kavkaz' (K), 'Amigo' (A), 'OH414,' 'OH416,' and 'GR876.' *Large arrow* (on *left*) points in the direction of movement of faster-moving bands. *Arrows* (on *right*) indicate distinctive secalin bands, while *smaller arrows* indicate other possible secalin bands

Table 3. Meiotic configurations of 43-chromosome hybrids produced using 'Chinese Spring' dimonotelosomic-*1B*

Female parent	No. of plants analyzed	No. of PMCs observed	Meiotic configuration			
			$19''+tL1''+2'+tS'$	$20''+tL1''+tS'$	$20''+(tS+tL)1'''$	$18''+tL1''+1^{IV}+tS'$
'Kavkaz'	1	18	1	17	–	–
'GR876'	1	18	–	3	–	15
'OH413'	2	39	1	34	–	4
'OH414'	3	38	2	36	–	–
'OH416'	3	42	3	15	24	–

chromosome *1B* to form a telosomic trivalent (Fig. 1c). In all other hybrids involving 'Kavkaz,' 'GR876,' 'OH413,' and 'OH414,' the short-arm telosome remained unpaired, while the long-arm telosome formed a bivalent with the translocation chromosome (Fig. 1d). As further evidence of reciprocal chromosome translocations between 'GR876' and 'Chinese Spring,' quadrivalents were again observed in most PMCs from the 'GR876' hybrid.

Electrophoretic analyses

Several protein bands, identifiable as rye secalin bands by comparing the band pattern from 'Chinese Spring' to those from '2a' rye and the 'Imperial' *1R* addition line of 'Chinese Spring,' exist among the gliadins of check cultivars 'GR876,' 'OH414,' and 'OH416' (Fig. 2). The slowest-moving secalin band is common to the check cultivars 'GR876,' 'OH414,' and 'OH416.' However, three faster-moving secalin bands are unique to 'Veery,' 'Kavkaz,' 'GR876,' and 'OH414.' 'Amigo' and 'OH416' have two bands (Fig. 2, small double arrows) not easily distinguished as secalin bands, although '2a' rye also appears to have the slower-moving of these two bands (Fig. 2, small single arrow). A band pattern for 'OH413' is not included in Fig. 2; however, additional electrophoretic samples indicated that secalin bands for 'OH413' also migrated similarly to those for 'Veery', 'Kavkaz,' 'GR876,' and 'OH414.' All patterns in Fig. 2 proved to be representative of each cultivar and line, since few kernels exhibited different patterns when additional samples were run.

Discussion

Wheat chromosomes *1B* and *6B* have distinctive secondary constrictions in their short arms. Hence, four satellited chromosomes can often be observed in somatic root-tip cells of euploid 42-chromosome wheats. The satellite in the short arm of chromosome *1R* is not expressed in a wheat background (Merker 1973). Therefore, when *1RS* replaces the short arm of chromosome *1B*, two satellited chromosomes, instead of four, are often observed in mitotic root-tip cells. This phenomenon has helped identify wheat cultivars carrying a *1RS/1BL* chromosome translocation (Mettin et al. 1973; Merker 1982).

Observations that root-tip cells of 'GR876,' 'OH413,' and 'OH414' mostly have two satellited chromosomes suggest that they carry a *1RS/1BL* translocation. Conversely, the observation that root-tip cells of 'OH416' mostly have four satellited chromosomes suggests that it does not carry a *1RS/1BL* translocation. The few observations of more than two satellited chromosomes for

'Kavkaz,' 'GR876,' 'OH413,' and 'OH414' were likely due to the detection of less conspicuous secondary constrictions in chromosomes other than *1B* and *6B*. Heteromorphic bivalents, such as those observed in hybrids where one parent had a *1RS/1BL* translocation (Zeller 1973), were frequently seen in PMCs from hybrids involving 'Kavkaz,' 'GR876,' 'OH413,' and 'OH414,' confirming the presence of the *1RS/1BL* translocation. No heteromorphic bivalents were observed in hybrids involving 'OH416,' as was the case for hybrids involving the check cultivar, 'Amigo,' which is known to lack a *1RS/1BL* translocation but carries a *1RS/1AL* translocation (Zeller and Fuchs 1983). Observations of PMCs from 43-chromosome hybrids, produced using 'GR876' and the Ohio lines in combination with 'Chinese Spring' dimonotelosomic-*1B*, further substantiate the presence of a *1RS/1BL* translocation in 'GR876,' 'OH413,' and 'OH414,' as well as its absence in 'OH416.' Only hybrids involving OH416 exhibited a meiotic configuration in which *1BS* and *1BL* telosomes formed a trivalent with chromosome *1B*. In all other hybrids, telosome *1BL* paired with the translocation chromosome and telosome *1BS* remained unpaired. This is a configuration that has been observed in hybrids involving cultivars carrying *1RS/1BL* translocations, since *1BL* pairs with the translocation chromosome and *1BS* does not pair with *1RS* (Cai and Liu 1989). In addition to its *1RS/1BL* translocation, 'GR876' likely contains reciprocal translocations compared to 'Chinese Spring.' Hybrids involving 'GR876' and 'Chinese Spring' derivatives had PMCs in which quadrivalents were consistently observed along with a heteromorphic bivalent.

Gliadin proteins, extracted from individual kernels of the check cultivars, 'GR876,' and the advanced Ohio lines, contained rye secalins, which appeared as distinctive bands when separated by polyacrylamide electrophoresis. These secalin bands migrated similarly to the fast-moving ω-secalins identified by Dhaliwal et al. (1987). The ω-secalins were shown by Shewry et al. (1986) to be controlled by the *Sec-1* gene locus on the short arm of chromosome *1R*. Hence, each cultivar and Ohio line, including 'OH416,' which was shown cytologically to lack a *1RS/1BL* translocation, carry at least a portion of the short arm of chromosome *1R*. Secalin bands from 'GR876,' 'OH413,' and 'OH414' matched the migration pattern of secalins from 'Veery' and 'Kavkaz.' Possible secalin bands from 'OH416' matched the migration pattern of those from 'Amigo.' It is interesting that three secalin bands present among the gliadins of 'Veery,' 'Kavkaz,' 'GR876,' and 'OH414' are lacking from 'OH416' and 'Amigo,' since the short arm of chromosome *1R* is present in both the 'Amigo' and 'Kavkaz' translocations.

There are three possible explanations for the failure of these secalins to be expressed by the 'Amigo' translocation. First, it is possible that the 'Amigo' translocation involves a smaller *1RS* segment than the 'Kavkaz' translocation. Second, perhaps the fact that each segment is derived from a different original rye source results in the expression of different secalin genes. The rye source for the 'Amigo' translocation was 'Insave' rye (Sebesta and Wood 1978), whereas the source for the 'Kavkaz' translocation was 'Petkus' rye (CIMMYT 1989). The slower-moving band of two possible secalin bands unique to 'Amigo' and 'OH416' did appear to migrate similar to a band from '2a' rye (see arrow in 'R', Fig. 2). A third possible explanation is that the 'Amigo' translocation involves wheat chromosome *1A*, whereas the 'Kavkaz' translocation involves *1B* and expression of wheat ω-gliadin genes on chromosome *1BS* may effectively suppress the expression of homoeologous secalin genes carried by the Amigo translocation. The latter two explanations are favored, since the 'Amigo' and 'Kavkaz' translocations involve the entire *1RS* arm (Lapitan et al. 1986; Mettin et al. 1978) and likely originated from the misdivision of univalents as described by Morrison (1954). Lukaszewski and Gustafson (1983) demonstrated that many rye/wheat translocations can result from such misdivisions, producing translocations involving whole rye chromosome arms. In addition, since the *Sec-1* locus is distally located on *1RS* (Lawrence and Appels 1986), both translocations likely carry all ω-secalin genes. Shewry et al. (1986) reported that genes for ω-secalins were homologous even between two rye species. However, Shepherd and Jennings (1971) attributed secalin band pattern differences between a wheat/rye amphiploid and its parents to rye genotype differences or interactions between rye and wheat proteins.

Since 'Kavkaz' is in the pedigrees of 'GR876,' 'OH413,' and 'OH414,' while 'Amigo' is in the pedigree of 'OH416,' one can conclude that 'GR876,' 'OH413,' and 'OH414' inherited the *1RS/1BL* translocation from 'Kavkaz,' while 'OH416' inherited the *1RS/1AL* translocation from 'Amigo.' A. Lukaszewski (personal communication) has confirmed these translocations independently by C-banding chromosomes from 'GR876' and the advanced Ohio lines.

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