

Cytology of Monosomic Rye (*Secale Cereale* L.) Substitutions in Wheat (*Triticum Aestivum* L.) with Reference to Univalent Behaviour¹

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In wheat rye substitution program, it has been experienced (Jenkins 1966) that when monosomic substitutions ($20''W+1'W+1'R$; 'W' and 'R' stand for wheat and rye chromosomes respectively) are selfed, the disomic substitutions are obtained at a very low frequency. There could be 2 possible reasons for this situation, 1) that the rye univalent is more often eliminated during meiosis, as a result of which the frequency of gametes having rye chromosome is very low, or 2) that the gametes having rye chromosome are at a definite disadvantage, as a result of which the transmission of gametes having rye chromosome is very low (Gupta 1967, 1968). Perhaps each of these factors accounts partially for the inability to get the disomic substitutions in the expected frequencies.

The cytology of 21 F_1 lines of $20''W+1'W+1'R$ constitution was worked out in order to find out if the rye univalent behaves different from the wheat univalent during meiosis. The results of these investigations are presented in this paper.

Material and methods

Twenty one different F_1 lines of $20''W+1'W+1'R$ constitution were obtained in a substitution program by crossing 7 wheat (*Triticum aestivum* var. Kharkov) monosomics of the D genome with 3 addition lines for rye (*Secale cereale* var. Dakold) chromosomes I, IV and V (designated after Bhattacharyya and Jenkins 1960). These 21 lines were also reciprocally crossed with normal wheat plants in order to determine the transmission of the products of misdivision of the univalents i.e. telocentric chromosomes and isochromosomes.

For mitosis, the technique outlined by Tsunewaki and Jenkins (1960) was followed. For meiosis, spikes were fixed in Carnoy's fluid (6:3:1) and anthers were squashed in 0.5% solution of acetocarmine.

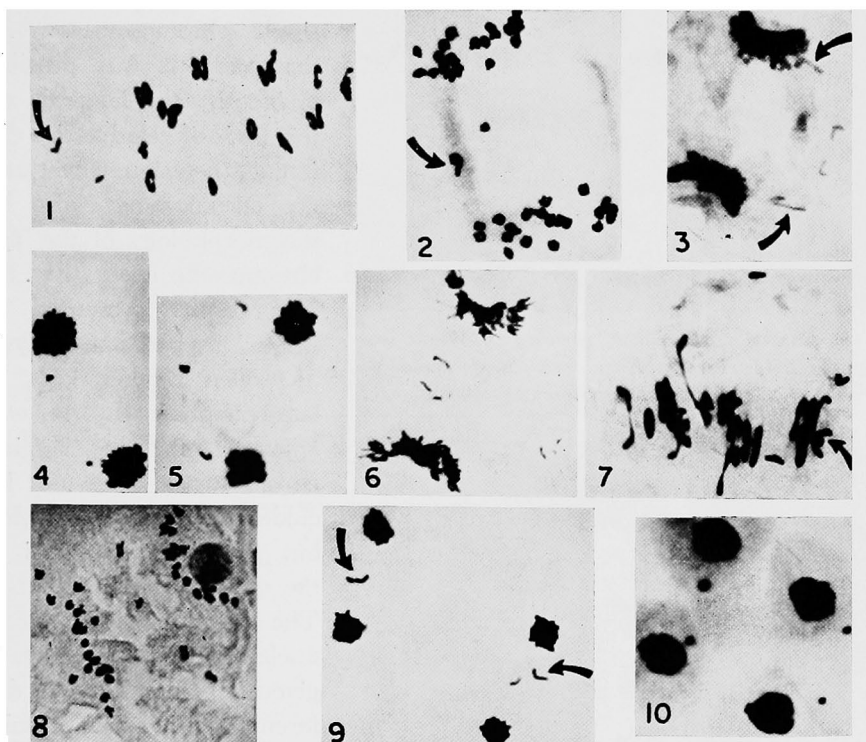
The rye chromosomes were identified on the basis of their distinct morphology (Bhattacharyya and Jenkins 1960).

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Results

Several plants which proved to be of the constitution $41W+1R$ at mitosis were studied at meiosis and were found to exhibit a configuration predominantly of $20''W+1'W+1'R$ (Fig. 1). At metaphase 1, the 2 univalents were usually found outside the equatorial plate. As most commonly observed at early anaphase I, the bivalents were regularly disjoined, with 20 chromosomes moving to each pole and the 2 univalents lagging at the plate (Fig. 2).



Figs. 1-10. Meiosis in monosomic rye substitutions ($41W+1R$). 1, metaphase I showing $20''W+1'W+1'R$. 2, anaphase I showing 20 chromosomes on each pole and 2 lagging univalents. 3, late anaphase I where both univalents have already divided. 4, lagging chromosomes fail to be included and form micronuclei. 5, at anaphase I only one univalent divided, wheat univalent undivided. 6, anaphase I showing misdivision of univalents. 7, metaphase I showing $19''W+3'W+1'R$. 8, anaphase I showing 19 chromosomes on each pole and 4 lagging univalents. 9, anaphase II showing lagging of 2 rye chromosomes and one wheat chromosome. 10, quartet stage showing 4 micronuclei. (All figures $\times 360$; arrow indicates rye chromosome).

Usually the 2 univalents divided at anaphase I in a regular manner (Fig. 3) and were either included in the nuclei at telophase I or were excluded as micronuclei in the cytoplasm (Fig. 4). In addition the following variation in the univalent behavior was observed: 1) non-division of one of the 2 lagging univalents, a condition which was perhaps more common with wheat univalent (Fig. 5); 2) one or the other, or both univalents misdivided giving

rise to telocentric chromosomes and isochromosomes (Fig. 6).

In a small percentage of cells at metaphase I (5%) $19''W+3'W+1'R$ were observed due to asynapsis or desynapsis between 2 homologous wheat chromosomes (Fig. 7). This situation could lead to the presence of 4 lagging univalents observed at anaphase I (Fig. 8).

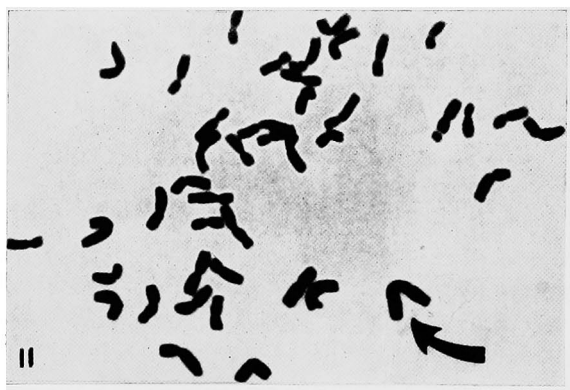
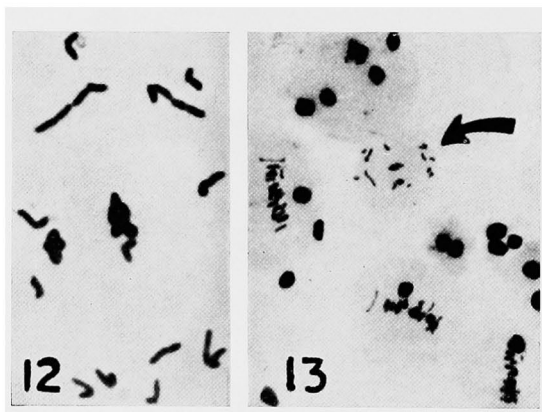


Fig. 11. Somatic metaphase showing $42W+1$ isochromosome for long arm of rye chromosome V. (Arrow indicates isochromosome; $\times 900$).



Figs. 12-13. Chromosome mosaics. 12, an abnormal pollen mother cell showing 3 bivalents and 16 univalents at metaphase I. ($\times 600$). 13, pollen mother cells showing the relative size of the abnormal cell shown in Fig. 12. (Arrow indicates abnormal cell). ($\times 140$).

At anaphase II, the laggards were not infrequent and consisted mainly of single chromosomes. At that stage it was possible to identify the laggards on the basis of relative size difference between wheat and rye chromosomes, also by the morphology of the rye chromosome itself (Fig. 9). The results presented in Table 1 are based on analysis of pollen mother cells at late anaphase II. It was apparent that the lagging chromosomes were not included in the pollen nuclei, but formed micronuclei at the quartet stage (Fig. 10). The frequency of micronuclei at the quartet stage is given in Table 2 for 4 different lines. The results in Table 1 did not include the doubtful cases where lagging chromosomes could not be identified with certainty. Therefore the actual frequency of quartets exhibiting no laggards was lower than observed in the

present study.

As a result of misdivision of the univalents telocentrics and isochromosomes originated. The frequency of telocentrics and isochromosomes in female transmission, male transmission and in selfed progenies is given in Table 3. Telocentrics and isochromosomes were identified at mitosis only (Fig. 11). For rye chromosome I, isochromosomes must have escaped detec-

tion at mitosis since both arms are similar. Wheat isochromosomes must have escaped detection for similar reasons. Therefore the isochromosomes recorded in Table 3 belong to only rye chromosomes. Telocentrics scored belong to both wheat and rye chromosomes and have been grouped.

Table 1. Distribution of lagging chromosomes at anaphase II and telophase II in 20''W+1'W+1'R plants

Line involved Lagging chromosomes	2DIV	3DIV	4DIV	5DIV	7DIV
0	25	12	7	2	6
1W	5	5	3	—	3
1R	10	9	3	5	1
2W	3	3	—	1	2
2R	8	5	3	1	5
1W+1R	4	7	2	2	3
1W+2R	5	2	5	1	5
2W+1R	1	2	4	1	2
2W+2R	14	6	3	2	2
Total quartets	75	51	30	15	29
Total laggards	36W+55R	36W+44R	24W+31R	11W+16R	23W+30R

Table 2. Frequency of quartets with different numbers of micronuclei in pollen mother cells in 20''W+1'W+1'R plants

Line involved Number of micronuclei	4DIV	5DIV	6DIV	7DIV	Total
0	121	154	39	138	452
1	163	173	39	152	527
2	256	145	72	116	589
3	88	38	12	24	162
4	49	19	3	16	87
Total	677	529	165	446	1817

Chromosome mosaics were also observed in one plant of chromosome constitution 20''W+1'W+1'R. About 10 cells each with 22 chromosomes exhibited a bivalent frequency ranging from 3-6 and univalent frequency of 10-16 (Fig. 12). These cells were smaller in size than the regular pollen mother cells in this line (Fig. 13).

Discussion

Considerable knowledge of the behaviour of univalents comes from the

study of haploids, polyhaploids and interspecific hybrids in the sub-tribe Triticinae (Riley and Chapman 1957). In addition valuable information has come from extensive work on aneuploid wheats by Sears (1954), on barley by Tsuchiya (1960), on maize by McClintock and Hill (1931), on tobacco by Clausen and Cameron (1944) and on oats by McGinnis (1962). Certain

Table 3. Frequencies of telocentrics and isochromosomes among female gametes, male gametes and selfed progenies of 20'W+1'W+1'R plants

Rye chrom- osome	Wheat chrom- osome	Female gametes			Male gametes			Selfed progenies		
		No. exam.	No. with telos.	No. with isos.	No. exam.	No. with telos.	No. w. isos.	No. ex.	No. w. telos.	No. w. isos.
I	1D	57	1	—	41	4	—	20	—	—
	2D	37	1	—	52	—	—	16	1	—
	3D	40	1	—	32	3	—	20	1	—
	4D	32	—	—	60	3	—	50	7	—
	5D	32	—	—	57	—	—	20	3	—
	6D	22	—	—	33	1	—	20	1	—
	7D	25	—	—	20	1	—	21	6	—
Total		245	3 (1.2%)	—	295	12 (4.1%)	—	167	19 (11.4%)	—
IV	1D	38	2	1	22	—	—	20	1	—
	2D	37	—	—	24	2	—	19	—	—
	3D	44	—	—	59	2	—	20	—	—
	4D	38	2	2	49	5	1	19	1	—
	5D	31	1	—	24	1	—	20	4	—
	6D	39	—	—	54	5	—	19	—	—
	7D	26	—	—	27	1	—	17	2	—
Total		253	5 (2.0%)	3 (1.2%)	259	16 (6.2%)	1 (0.4%)	134	8 (6.0%)	—
V	1D	27	1	—	31	2	—	24	5	—
	2D	20	—	—	30	1	—	23	1	—
	3D	19	1	—	29	1	—	24	1	—
	4D	22	3	1	43	4	1	18	—	1
	5D	24	1	—	43	2	1	24	3	—
	6D	48	4	—	51	1	—	21	4	—
	7D	12	—	—	31	7	—	21	4	1
Total		172	10 (5.8%)	1 (0.6%)	258	18 (7.0%)	2 (0.8%)	155	18 (11.6%)	2 (1.3%)

conclusions can be derived regarding the behaviour of univalents from these studies :

- 1) Univalents are distributed to the poles at random.
- 2) Univalents may pass to either pole without dividing at first division of meiosis and may subsequently divide normally at the second division.

- 3) There is a tendency for the univalents to either lag at the first division or divide at the first division and then lag at the second division. Usually the lagging chromosomes are not included in the nuclei resulting from meiosis, but appear as micronuclei in the quartet of spores.
- 4) Occasionally the univalents may divide at first division of meiosis and may again misdivide at the second division.

In the present investigation it has been observed that at anaphase I, the rye chromosome IV divides more often than wheat chromosome, as a result of which the rye chromosomes lag more often at anaphase II and form micronuclei at telophase II. However there is a close agreement between frequency of laggards at anaphase II and frequency of micronuclei at telophase II. The results presented in this paper for anaphase II and telophase II pertain to rye chromosome IV only. Similar results for other 2 chromosomes namely I and V were not recorded, but, from other information available from the distribution of the progeny of the monosomic addition lines, it was reasonably clear that the 3 rye chromosomes in question behave in the same manner (Gupta 1967). It was also apparent from these results that the majority of gametes were deficient for both the rye chromosome as well as the wheat chromosome. The reason for such a behaviour of rye chromosome is not known, but since it is a characteristic of the rye chromosomes, the size of the chromosomes and the structure and activity of the kinetochore of the rye chromosomes should be responsible for a more frequent division of the rye chromosome at anaphase I. Another possible reason for such a behaviour of rye chromosomes may be the different genetic background in which they are placed.

While studying the frequency of telocentric chromosomes and isochromosomes, an important observation was made. Sears (1954) observed in wheat monosomics that telosomes and isochromosomes are transmitted at a very low rate in male gametes except in case of long arm of IX. In the present study, the transmission of telos and isos was much higher in male than in female gametes. This suggested that the presence of telosome or isochromosome in a male gamete puts it at an advantage over 20 chromosome male nulli-gametes. Such competition is however not known among female gametes.

The chromosome mosaics like those reported here were also observed by Watanabe (1961, 1962) in wheat var. Shirhada. The cells having 22 chromosomes must have resulted at a premeiotic stage due to the division of the cells without corresponding division of the chromosomes. Such pollen mother cells would result in sterile pollens.

Summary

Meiosis in monosomic substitutions ($20''W + 1'W + 1'R$) was studied. Oc-

casionally 4 univalents were observed. The rye univalent divided more often than the wheat univalent at anaphase I, as a result of which the rye chromosome lagged more frequently at anaphase II. Telocentric chromosomes and isochromosomes were transmitted more frequently in male gametes than in the female gametes. Chromosome mosaics were also observed.

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