STADLER SYMPOSIA, VOL. 4 (1972) University of Missouri, Columbia -23-

CHROMOSOME ENGINEERING IN WHEAT[1]

E. R. SEARS

U. S. Department of Agriculture and
Agronomy Department, University of
Missouri, Columbia, Missouri 65201

SUMMARY

Three methods have been developed for the transfer of genetic material to wheat chromosomes from alien chromosomes:

(i) Use of ionizing radiation to translocate an alien segment.

(ii) Induction of homoeologous pairing, which may be followed by crossing over. This is the easiest and usually the most effective method, provided the alien chromosome is sufficiently closely related to one of its wheat homoeologues that frequent pairing can occur.

(iii) Exploitation of the tendency of univalent chromosomes to misdivide. Telocentrics resulting from simultaneous misdivision of two univalents have recently been shown to unite and to produce a new chromosome having one arm from each of the univalents.

INTRODUCTION

Because it is a hexaploid, with much triplication of genetic material, common wheat (*Triticum aestivum L.*) is especially favorable for use in experiments which involve gross changes in the chromosomes. Deficiencies or duplications for as much as an entire chromosome are transmitted through the egg without adverse selection and even pass through the pollen, as well, although usually in low frequency. The nullisomic and the tetrasomic have been recovered for each of the 21 chromosomes, and each is viable and to some extent fertile (SEARS 1954).

The chromosomes of wheat have proved to fall into seven groups of three each, reflecting the origin of wheat from three related diploids, each with seven pairs of chromosomes (SEARS 1958). Within each of these homoeologous groups of three, the chromosomes are so closely related that extra dosage of any one is able to compensate, at least in part, for complete absence of either of the other two (SEARS 1966b). The homoeologues normally show little or no tendency to pair, however, because of the activity of a pairing-

---

[1] Cooperative investigations of the Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture, and the Agronomy Department, Missouri Agricultural Experiment Station. Journal Series No. 6357 of the Missouri Station.

reducing gene on chromosome 5B. They can be induced to pair by removing chromosome 5B or by suppressing its effect on pairing by adding the chromosomes of certain diploid relatives, such as *Triticum (Aegilops) speltoides* (Tausch) Gren. ex Richter.

Not only do the chromosomes of wheat fall into seven distinct groups, but also the chromosomes of various related species are proving to fit into the same groups. Nearly every chromosome studied of Secale, Agropyron, and what was formerly designated Aegilops (now Triticum) has been found to fit into one, and only one, of the homoeologous groups.

Because the relatives of wheat have characteristics such as resistance to disease that are potentially useful in wheat breeding, there has been a great deal of effort directed toward transferring genes from the relatives to wheat. In recent years this has taken the form of transferring segments of alien chromosomes carrying particular desired genes to wheat chromosomes. This we may speak of as chromosome engineering. Although this term logically includes the induction of inversions and reciprocal translocations and other rearrangements, we shall here be concerned only with the transfer of alien segments to wheat chromosomes. Three techniques will be described, involving, respectively, the use of ionizing radiation, the induction of homoeologous pairing, and the exploitation of misdivision of univalent chromosomes.

TRANSFERS INDUCED BY IRRADIATION

Since ionizing radiation breaks chromosomes at random, and since the pieces then rejoin in ways that are often novel, it is clearly possible to use radiation to transfer an alien chromosome segment carrying a specific gene to a wheat chromosome. The difficulty is that unless the gene concerned is near one end of the alien chromosome, any easily obtained translocation will involve the transfer to the wheat chromosome of a long alien segment likely to include some unwanted genes as well as the desired one.

It is of course possible for the radiation to break out a small internal segment of the alien chromosome and for this to become inserted in a wheat chromosome, thus perhaps limiting the transfer of alien material to the gene desired and at the same time avoiding the loss of any wheat chromatin. Unfortunately such intercalary translocations are rare, and any practicable effort to recover one must be able to take advantage of a strongly favorable selective pressure.

A more realistic objective is to produce a reciprocal translocation in which the desired alien-chromosome segment replaces a corresponding segment of a homoeologous wheat chromosome. The alien segment may then compensate for the missing wheat segment, as well as introducing the desired alien gene. Although the chance that an alien segment will happen to be exchanged for a particular segment of a specific wheat chromosome may seem remote, there is evidence that such translocations occur preferentially (KNOTT 1968). As Knott pointed out, if homoeologues are associated to some extent in somatic cells, this would provide a ready explanation for the otherwise surprisingly frequent occurrence of such translocations.

The first attempt to use radiation to transfer an alien gene to a wheat chromosome (SEARS 1956) was designed to take advantage of a selection mechanism that would facilitate the recovery of desirable translocations. Plants were irradiated that had a single dose of a chromosome from *Triticum umbellulatum* (Zhuk.) Bowden (*Aegilops umbellulata)* carrying a gene for resistance to the leaf-rust fungus, *Puccinia recondita* Rob. ex Desm. Only about one-fourth of the pollen grains from these monosomic-addition plants carried the alien chromosome, and these grains functioned poorly, so that the chromosome was transmitted through pollen to only about 1.5% of the offspring. Irradiation of the plants previous to meiosis favored translocations in which the deleterious effect of the umbellulatum chromosome had been lost and no serious loss of wheat chromatin had occurred. This was because the ensuing meiotic division usually eliminated what remained of the umbellulatum chromosome, and pollen with an intercalary translocation or a compensating reciprocal translocation could compete on equal terms with normal pollen. By a simple test for resistance to the fungus, daughter plants that had failed to receive at least the critical portion of the umbellulatum chromosome were eliminated. Cytological study then showed which resistant offspring had the unchanged alien chromosome and which had only part of it, translocated to a wheat chromosome.

Of the 17 translocations identified in this experiment, only one proved not to be deleterious. At first this one was believed to be an intercalary translocation, but subsequent study showed that a sizeable umbellulatum segment had replaced the terminal portion of the long arm of wheat chromosome 6B (SEARS 1966a). ATHWAL and KIMBER (1972) have now shown that, as might have been expected, the umbellulatum chromosome and 6B are homoeologues. The homoeology is apparently less strong, however, than that between various other alien and wheat chromosomes where successful transfers have been effected (ACOSTA 1961, KNOTT 1961, DRISCOLL and JENSEN 1963, SHARMA and KNOTT 1966, WIENHUES 1966--see KNOTT 1971, for review). This perhaps accounts for the fact that although relatively few translocations have been obtained in most of the experiments with other chromosomes, each of these experiments has been successful in yielding one or more satisfactory transfers.

Where there is little or no selection against gametes carrying the entire alien chromosome, there is presumably no point to using a monosomic rather than a disomic addition line if transfers are to be detected cytologically. Use of the disomic insures that every offspring, instead of only about one in four, is potentially a carrier of a translocation. Irradiation of seeds instead of plants is technically easier, but then the sectors are so large that each translocation may be recovered more than once, possibly leading to wasted effort in identifying duplicates. Irradiation of pollen insures that no translocation is recovered more than once.

DRISCOLL and JENSEN (1963,1964) used a genetic method for identifying translocations. They irradiated seeds of what was effectively a disomic substitution line (with a pair of rye telocentric chromosomes taking the place of the missing arm of one pair of wheat chromosomes). The X_1 plants were allowed to self, and segregation for a marker gene was sought in the next generation. Where one of the alien chromosomes was involved in a translocation, a quadrivalent was formed at meiosis, with segregation such that some gametes lacked the marker gene (leaf-rust resistance) carried by the alien chromosome. Segregation in subsequent generations distinguished between the desired translocations and other aberrations, such as monosomy for the alien chromosome. This genetic method could well be used with disomic addition lines, provided the lines had little tendency to lose the alien pair of chromosomes. SHARMA and KNOTT (1966, see also KIMBER 1972) irradiated addition monosomics and identified transfers by their segregating 3:1 instead of the approximate 1:3 characteristic of addition monosomes.

TRANSFERS INDUCED BY HOMOEOLOGOUS PAIRING

The possibility of inducing homoeologous pairing by the removal of chromosome 5B or the suppression of its effect suggests a second method of transferring genetic material from alien to wheat chromosomes. Induced pairing and crossing-over of an alien chromosome with one of its wheat homoeologues would seem to offer an excellent chance of accomplishing the substitution of an alien segment for a closely related wheat segment. Such a substitution might well have no deleterious effects, particularly if the alien gene desired was near the end of an arm, permitting transfer of the gene through exchange of only a short, terminal segment. Even if the gene was far from the end of the arm, transfer of a small segment might take place as a result of double crossing-over.

The likelihood of success using induced homoeologous pairing will vary with the alien chromosome concerned, for not only must this chromosome be able to pair homoeologously with one or more wheat chromosomes, but presumably it must also pair in the right region or regions. Some alien chromosomes (for example, those of *Agropyron elongatum* that have been tested; see JOHNSON and KIMBER 1967, and data to follow here) are capable of pairing rather freely with their wheat homoeologues, but others, particularly those of rye, remain of doubtful pairing ability (RILEY and KIMBER 1966).

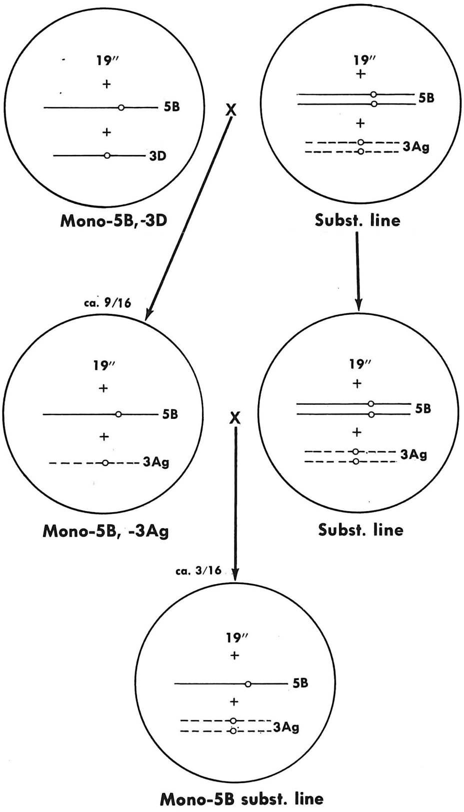

FIGURE 1. Method of obtaining monosomic-5B substitution line.

The simplest way to induce homoeologous pairing of alien chromosomes is to pollinate monosomic 5B by the alien species concerned. About 75% of the offspring are then deficient for chromosome 5B, and pairing occurs of alien with wheat chromosomes. These hybrids are likely to be highly sterile but may set a low percentage of seed on pollination by euploid wheat. Some of the chromosomes recovered may be recombined wheat-alien chromosomes. RILEY and KIMBER (1966) mentioned several characteristics believed to have been transferred to wheat through homoeologous chromosome pairing in a mono-5B X *T. bicorne* Forsk. *(Ae. bicornis)* hybrid.

Advantage can be taken in various ways of the ability of *T. speltoides* to suppress the activity of chromosome 5B and thereby allow homoeologous pairing. RILEY, CHAPMAN and JOHNSON (1968) crossed speltoides with a line that had an added chromosome from *T. comosum* (Sibth & Sm.) Richter *(Ae. comosa)*. Although the hybrid was nearly sterile, they were able to obtain a few offspring by crossing to euploid wheat, and they recovered a part-comosum, part-2D chromosome that conditioned resistance to the stripe-rust fungus, *Puccinia striiformis* West.

Another way to exploit the ability of *T. speltoides* to suppress 5B action was suggested by RILEY and KIMBER (1966). This is to cross an alien-substitution line to an amphiploid of *T. aestivum* x *T. speltoides*. In the hybrid both the alien chromosome and its wheat homoeologue are monosomic and thus free to pair with each other with no competition from homologous chromosomes.

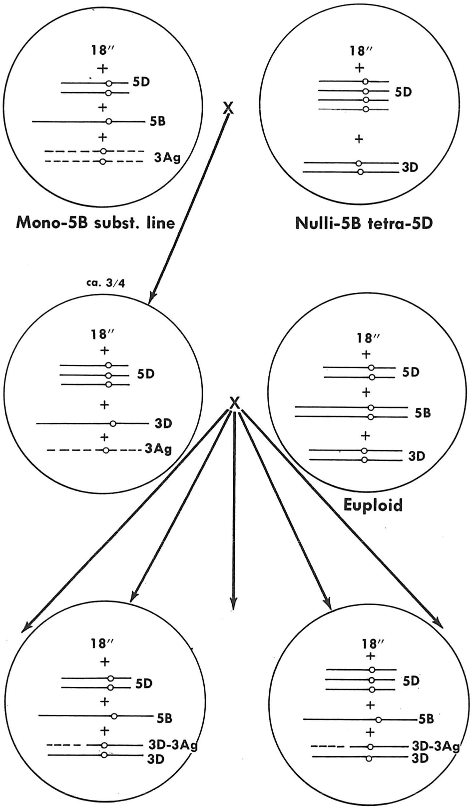

FIGURE 2. Method of inducing homoeologues to pair and of recovering recombined (translocated) chromosomes.

The method I have used (suggested by SEARS 1967) also involved the use of an alien substitution line. There were two of these, involving two different chromosomes of *Agropyron elongatum*, each of which conditioned resistance to the leaf-rust fungus. One chromosome was substituted for wheat chromosome 3D and the other for 7D. The 3D substitution line, which was developed at Oklahoma State University (BAKSHI and SCHLEHUBER 1959), is known as TAP 67. The other line originated at Purdue University (CALDWELL *et al.* 1956) and is called Agrus. It was identified as a 7D substitution by QUINN and DRISCOLL (1967).

Each addition line was first made monosomic 5B by crossing to mono-5B, mono-3D (or -7D) and back-crossing once to the addition line (Figure 1). The plants were then pollinated (Figure 2) by nullisomic-5B, tetrasomic-5D (the added dosage of 5D being needed to render nulli-5B fertile). Eight of the nine offspring proved to be nulli-5B. They were also trisomic-5D, monosomic-3D (or -7D), and monosomic for the Agropyron chromosome (hereafter designated 3Ag or 7Ag).

Both 3Ag and 7Ag could be seen to pair with the corresponding wheat chromosome, 3D or 7D, in the nulli-5B plants (Figure 3b). The tendency of chromosomes to clump in this material prevented determination of the precise frequency of pairing, but it was clear that pairing occurred in at least 10% of the microsporocytes. If the exact frequency had been ascertainable, an accurate prediction could have been made of the frequency with which a part-wheat, part-Agropyron chromosome carrying the leaf-rust resistance gene would be recovered, for each pairing event results in one such chromosome. With 10% pairing, 2.5% of gametes would carry such a chromosome, and about 9% of the resistant offspring would owe their resistance to a translocated chromosome. As will be seen, the number of translocations recovered was much higher than 9%; and it appears that about 30% pairing of 3D with 3Ag and of 7D with 7Ag actually occurred.

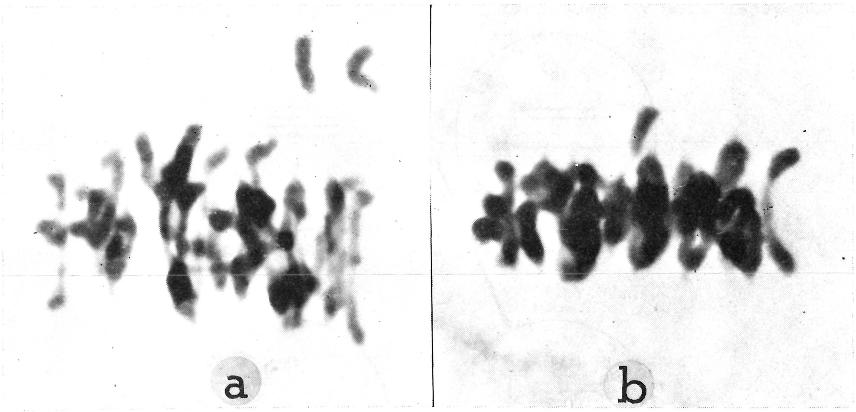

FIGURE 3. MI in nullisomic-5B, trisomic-5D, monosomic-7D, monosomic-7Ag. The two monosomes are unpaired in (a) and paired in (b).

The nulli-5B plants were pollinated by euploid, and the next two generations were crossed, as males if possible, to euploid.

With the 3Ag-for-3D substitution, 77 of the 299 offspring of the five nulli-5B plants possessed the marker gene, resistance to the rust fungus, and 25 of these had probable 3Ag-to-3D transfers (Table 1). Not all of the 25 were identifiable in the first generation, because of the presence of trivalents which, if they represented trisomes, involved only one kind of chromosome, but if they were three-chromosome translocations, involved two different chromosomes. In the former case, all the chromosomes might be accounted for as wheat chromosomes (including one with a resistance-bearing Agropyron segment), while in the latter instance, one univalent would be the unchanged Agropyron chromosome. Also, a few plants had the critical arm of the Agropyron chromosome present as a relatively unstable telocentric (formed as a result of misdivision at meiosis), and this telocentric happened to be present in the part of the plant tested for resistance but had been lost from the part examined cytologically.

Four of the 25 probable translocations were not recovered in the second or third generation. Among the 21 remaining, there were apparently significant differences in male transmission (Table 2). Most clustered in the 40% to 60% interval, clearly not significantly different from 50%; but three had less than 20% transmission. Also, several translocation chromosomes (all with reasonably good male transmission) proved to be capable of pairing in both arms with their homologue, thus demonstrating that less than an entire arm of 3Ag had been transferred. No doubt some of those not observed to pair in both arms are capable of doing so, but this is unlikely to be true of all.

Table 1. Analysis of offspring of nullisomic-5B, trisomic-5D, monosomic-3D, monosomic-3Ag plants pollinated by euploid.

Number of offspring, total	299
Resistant, total	77
Cytologically analyzed	74
Unchanged 3Ag	45
Probable telocentric 3Ag	4
Probable translocations, not recovered	4
Presumed 3D-3Ag transfers	21

In order that the translocations may be further characterized, each has been crossed to monosomic 3D, so that the transfer chromosome can be obtained monosomic. The morphology, vigor, and fertility of the hemizygous plants should indicate which transfers, if any, are non-deleterious. Also, tests of their progeny will establish whether or not the translocated chromosome actually is 3D, for if the resistance gene is carried by the 3D monosome, few or no susceptible individuals should segregate.

Results with the 7Ag chromosome were very similar (Tables 3 and 4). Only 138 offspring were obtained from the three nulli-5B, tri-5D, mono-7D, mono-7Ag plants available, but a larger fraction of these, totalling 48, were resistant. Thirteen of these had probable 7D-7Ag transfers, of which one was not recovered.

Male transmission of the 7Ag transfers was better than with 3Ag. Several had more than 50% transmission in each of the two generations, and for two of these (nos. 1 and 2) the departure from 50% was statistically significant. As with 3Ag, there were some that transmitted substantially less than 50%. Several transfer chromosomes paired in both arms with their wheat homologue, indicating relatively short Agropyron segments.

Crosses have been made to mono-7D for further characterization of the translocated chromosomes.

Table 2. Male transmission of presumed 3D-3Ag transfers.

Designation Ag3D-	First generation					Second generation					Third generation
	Aberrations			Offspring no.	Transmission %	Aberrations			Offspring no.	Transmission %	
	IV	III	I			IV	III	I			
1	1		1	9	88.8	1			27	59.3	21"
2		2	2	20	45.0				28	60.7	21"*
3	1		1	19	36.8				42	54.8	21"*
4		1	1	26	52.7	1			42	45.2	21"
5		1	2	9	33.3	1			49	49.0	21"
6	1	1	1	20	30.0				41	48.8	21"*
7		1	3	20	30.0				37	48.7	21"
8	1		1	29	55.2				43	39.5	21"
9	1		1	15	37.5	1			39	43.6	21"
10	1		1	27	33.3				23	43.5	21"*
11	1		2	8	25.0				43	44.2	21"
12	2		2	2	0.0	1	1	1	41	43.9	19"+1"' +1'
13	2	2	2			1	1		50	40.0	21"*
14	1	1	1	17	29.4				51	35.3	21"*
15		1	1	19	47.3				33	30.2	21"
16		1	2	11	54.5				47	25.6	21"
17		1	2	25	44.0		1	1	24	25.0	20"+1'
18	1	1	1	27	18.5				44	31.4	21"
19	1	2	2			1	1		21	19.0	19"+1^{IV}
20			3	18	27.8				59	15.2	21"
21	1	1	1	19	26.4				56	12.5	21"
Control			3**	14	35.0						
Control	1		3**	34	0.0						

*All ring bivalents in some cells.
**Includes one 3Ag monosome.

Table 3. Analysis of offspring of nullisomic-5B, trisomic-5D, monosomic 7D, monosomic-7Ag plants pollinated by euploid.

Number of offspring, total	138
Resistant, total	48
Cytologically analyzed	46
Unchanged 7Ag	33
Probable translocations, not recovered	1
Presumed 7D-7Ag transfers	12

Table 4. Male transmission of presumed 7D-7Ag transfers.

Designation Ag7D-	First generation					Second generation					Third generation
	Aberrations			Offspring no.	Transmission %	Aberrations			Offspring no.	Transmission %	
	IV	III	I			IV	III	I			
1			1	20	75.0				9	88.9	21"
2			2	16	75.0				50	64.0	21"*
3		1	1	22	54.4				51	66.7	21"
4		1	3						43	69.8	21"
5	2**	1	2	9	33.3	1			54	66.7	21"*
6	1		1	6	100.0				43	53.5	21"*
7		1	2	15	60.0				23	47.9	21"*
8	1		1	3	66.7	1			51	45.1	20"+t1"
9	1	1	1	18	55.6				46	45.6	21"*
10	1		1			1			48	37.5	21"*
11	1	3	2	4	0.0				43	30.3	21"
12	2	1	1			1		1	23	21.7	19"+1 '
Control	1	1	2***	37	10.8						

*All ring bivalents in some cells.
**Includes one hexavalent.
***Includes one 7Ag monosome.

TRANSFERS INDUCED BY UNION OF TELOCENTRICS

A third method of transferring part of an alien chromosome to a wheat chromosome is to allow a telocentric for one arm of the alien chromosome to combine with a wheat telocentric following misdivision of two monosomes. If the alien arm replaces a homoeologous arm, or if the alien arm is non-deleterious and replaces a non-essential wheat arm, the transfer chromosome may well be useful.

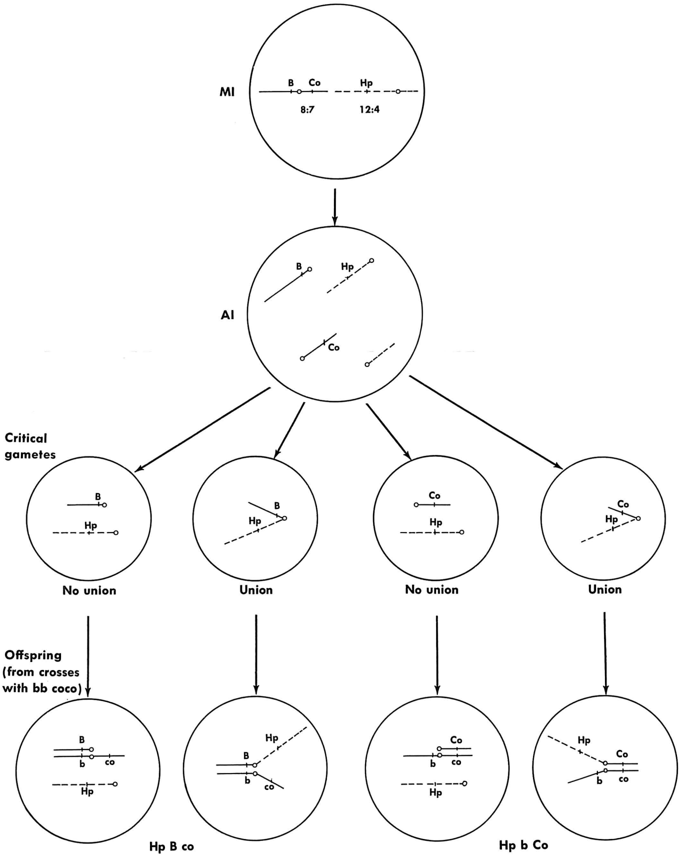

FIGURE 4. Method of obtaining translocations following misdivision of univalents.

It is well known that established telocentric chromosomes do not ordinarily join with each other to form bibrachial chromosomes. Many wheat lines with two telocentrics have existed for several generations, with no such union having been observed. There is no obvious reason, however, why two freshly formed telocentrics might not join. Indeed, MORRISON (1954) some years ago suggested such a mechanism to explain a translocation having one member telocentric, which he observed in an offspring of a monosomic; but homoeologous pairing could not be ruled out as the cause of the translocation. Subsequently MURAMATSU (1968 and private communication) found two translocations of rye chromosome 5R with wheat 5D and one with 5B which are difficult to explain except by misdivision and telocentric union; and SEARS (1969) obtained a 2A-2R translocation that also seems best explained as the result of misdivision.

Since the experiments of Muramatsu and Sears involved exchange between homoeologous chromosomes, it is very difficult to rule out the possibility of homoeologous pairing and crossing over, even though rye chromosomes have never been observed to pair with wheat chromosomes when chromosome 5B was present, as it was in these experiments. Clearly what is needed is to recover translocations between two non-homoeologous monosomes. Therefore an experiment was performed using chromosomes 6B and 5R.

Table 5. Classification of functioning gametes from double-monosomic 5RL, 6B marked with *Hp*, *B*, and *Co*.

Markers present	No. plants	Cytologically examined		
		No. plants	5R constitution	6B constitution
Hp B (Co?)	11	7	telo-L	complete
Hp B --	2	1	telo-L	iso-L
		1	6B transl.	5R transl.
Hp - (Co?)	3	1	telo-L	iso-S
		1	telo-L	none
Hp - --	5			
-- B (Co?)	39			
-- - (Co?)	32	1	none	none
-- - --	23			
Total	115			

The long arm of the 6B chromosome used was marked by the gene *B*, an awn suppressor, and the short arm by *Co*, which suppresses a leaf necrosis called corroded (Figure 4). The long arm of 5R carried *Hp* (Hairy peduncle). Double-monosomic 6B, 5R plants were pollinated by euploid wheat homozygous for *b* and *co* and of course lacking 5R. Thus the phenotype of the offspring showed the presence or absence of the long arm of 5R and both arms of the other maternal monosome, 6B.

In a preliminary experiment (Table 5) the single mono-6B, -5R plant available had a telocentric for the long arm of 5R rather than a complete 5R. Further, the expression of *co* was irregular, so that a few presumably corroded plants were of normal phenotype. Because of this, 7 of the 11 plants which were *Hp*, *B* and apparently *Co* were examined cytologically. All had an entire maternal-6B, and hence must have been genetically *Co*. Of the three plants that were *Hp*, *b*, and phenotypically *Co*, one had an isochromosome for 6B short, one completely lacked the maternal 6B (thus was genetically *co*), and the third was not examined cytologically. Of the two plants that were *Hp*, *B*, and *co*, one had an iso-6BL and the other had a 6BL-5RL translocation.

Although the 6BL-5RL chromosome could presumably only have arisen following misdivision of univalents and union of the resulting telocentrics, confirmation was sought in two more experiments, in both of which both monosomes were complete. In these experiments classification for corroded was reasonably good.

Although nearly 400 plants were grown in the two experiments (Table 6), only three individuals were found which had *Hp* together with only one arm of 6B. All three were deficient for 6BS. Two of the three proved to have the complete 5R, but the third lacked 5RS and in fact had a 6BL-5RL translocation. The plant had 21 bivalents, of which one was heteromorphic, with the 5RL arm being clearly identifiable by its conspicuous secondary constriction (Figure 5). This confirms the ability of freshly formed telocentrics to join.

The data are not extensive enough to permit a conclusion as to how frequently such translocations may be recovered from two monosomes. However, some idea of the maximum frequency may be gained from a consideration of the frequency with which telocentrics can be recovered from monosomic 5A (SEARS 1952). For the long arm of 5A, 2.5% of gametes carried a telocentric. The probability of a telocentric for a particular arm of each of two chromosomes would therefore be only .025 x .025 = .000625 - one in 1600. In the present experiment telocentrics for both arms of 6B could be identified, giving a probability of 5.0% for one or the other. Chromosome 5R probably has a rate of misdivision somewhat higher than does 5A, possibly leading to a rate of 5.0% production of telo-5RL. The probability of a telo-5RL and either a 6BS or a 6BL being included in the same nucleus may therefore have been as much as .05 x .05 = .0025, or one in 400. This would bring the present experiment into line, since one translocated chromosome was obtained in a population of 384 (excluding the preliminary experiment, where 5R was already telocentric).

Table 6. Classification of functioning gametes from double-monosomic 5R, 6B marked with *Hp*, *B*, and *Co*.

Markers present	No. plants Exp. 1	Exp. 2	Cytologically examined No. plants	5R constitution	6B constitution
Hp B Co	6	27	4	complete	complete
			3	telo-L	complete
			2	iso-L	complete
Hp B --	1	2	1	complete	telo-L
			1	complete	iso-L
			1	6B transl.	5R transl.
Hp - --	13	69	1	telo-L	none
-- B Co	27	60			
-- B --	2	3			
-- - Co	5	3			
-- - --	48	118			
Total	102	282			

The agreement between calculated telocentrics and observed translocations might be taken to suggest that every time two new telocentrics are included in the same nucleus, they join to form a bibrachial chromosome. Such a conclusion is strengthened to some extent by the fact that in the present experiments no plant was recovered that had two telocentrics; in other words, in the only two plants that had but one arm each of 6B and 5R, the two arms had joined.

The foregoing suggests that there is at least a strong tendency for newly produced telocentrics to join. The calculations of expected frequency cannot be taken very seriously, however, particularly for extension to other material. The frequency of misdivision certainly varies with the genetic background, and it probably differs from chromosome to chromosome with the same background. Further, the 5A data used were based on recovered telocentrics, whereas one knows from the work of STEINITZ-SEARS (1966) that probably the majority of telocentrics formed are not recovered but are unstable and suffer loss before the plant matures. On the other hand, telocentrics are produced at both the first and second reduction division, and there is no assurance that a telocentric arising at the first division can join with one produced at the second.

FIGURE 5. Heteromorphic bivalent (second from right) consisting of a normal 6B chromosome (above) and a 6B-5RL translocation chromosome. Note the pronounced secondary constriction in the free (5RL) arm of the translocation chromosome.

Although the rate of production of translocations following misdivision of two univalents may be very low, the rate may become substantial when several univalents are present, as in haploids and certain hybrids. When haploids of wheat are pollinated by diploids, translocations are recovered among the offspring. OKAMOTO and SEARS (1962) assumed that these were all the result of pairing and crossing over, even though four of the 13 studied proved to involve non-homoeologous chromosomes. Probably these four translocations were produced by union of telocentrics formed by misdivision of univalents.

Some alien chromosomes (for example, those of rye) do not substitute with full success for their wheat homoeologues and do not pair readily, if at all, with their homoeologues, even in the absence of 5B activity. In these cases the introduction of an alien arm through telocentric union may be worth attempting. Chromosome 2R of rye substitutes poorly for 2A; in fact, the 2R-for-2A substitution disomic is almost completely sterile. But plants disomic for a 2AS-2RL chromosome, presumably formed by misdivision and telocentric union, are relatively vigorous and fertile (Figure 6). It is not known that 2RL carries any useful genes, but if it does, whole-arm substitution through telocentric union may be a practical way of introducing them.

In addition to their possible practical value, new chromosomes formed by union of telocentrics are of considerable interest in studies of the centromere. Most or possibly all such chromosomes have essentially hybrid centromeres. Also, different new chromosomes involving the very same arms may well have centromeres differing in the amount of material contributed by the two parental centromeres, for STEINITZ-SEARS (1966) has shown that misdivision-induced breaks probably occur at different places along the length of the centromere. The amount of centromere material, as well as which chromosome it comes from, could very well affect a chromosome's behavior, particularly with respect to the frequency with which it misdivides when univalent.

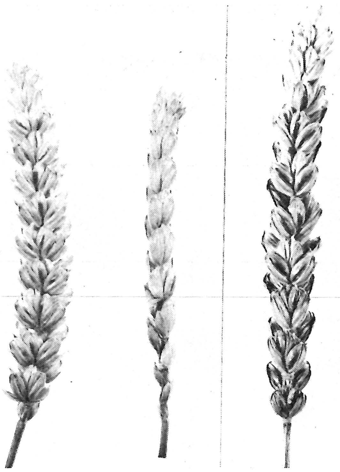

FIGURE 6. Spikes of (left) normal wheat, (center) disomic substitution of rye chromosome 2R for wheat chromosome 2A, and (right) disomic substitution of the long arm of 2R for the long arm of 2A (that is, disomic for a translocated 2A-2R chromosome).

One common type of evolution involves a reduction in the number of chromosomes through union of the long arms of strongly acrocentric chromosomes to form metacentrics, with attendant loss of the short arms. This is assumed to occur through breakage of two acrocentrics near to, but outside of, the centromere, followed by reunion. Obviously, as MORRISON (1954) pointed out, the union of telocentrics following misdivision of univalents is another way of accomplishing the same thing. Judging from the experiment with 6B and telo-5RL, the chromosomes concerned could be true telocentrics, rather than acrocentrics, and still undergo misdivision and subsequent union.

LITERATURE CITED

ACOSTA, A. 1961 The transfer of stem rust resistance from rye to wheat. Ph.D. Thesis, Mo. Univ.:56 pp.

ATHWAL, R. A., and G. KIMBER 1972 The pairing of an alien chromosome with homoeologous chromosomes of wheat. Canad. J. Genet. Cytol. (in press).

BAKSHI, J. S., and A. M. SCHLEHUBER 1959 Identification of a substituted chromosome pair in a Triticum-Agropyron line. Proc. Okla. Acad. Sci. *39*:16-21.

CALDWELL, R. M., J. F. SCHAFER, L. E. COMPTON, and F. L. PATTERSON 1956 Resistance to leaf rust derived from Agropyron elongatum. Rept. 3rd Int. Wheat Rust Conf.:95-96.

DRISCOLL, C. J., and N. F. JENSEN 1963 A genetic method for detecting intergeneric translocations. Genetics *48*:459-468.

DRISCOLL, C. J., and N. F. JENSEN 1964 Characteristics of leaf rust resistance transferred from rye to wheat. Crop Sci. *4*:372-374.

JOHNSON, R., and G. KIMBER 1967 Homoeologous pairing of a chromosome from Agropyron elongatum with those of Triticum aestivum and Aegilops speltoides. Genet. Res., Camb. *10*:63-71.

KIMBER, G. 1972 The design of a method, using ionising radiation, for the introduction of alien variation into wheat. Indian J. Genet. & Pl. Breed. (in press).

KNOTT, D. R. 1961 The inheritance of rust resistance. VI. The transfer of stem rust resistance from Agropyron elongatum to common wheat. Canad. J. Plant Sci. *41*:109-123.

KNOTT, D. R. 1968 Translocations involving Triticum chromosomes carrying rust resistance. Canad. J. Genet. Cytol. *10*:695-696.

KNOTT, D. R. 1971 The transfer of genes for disease resistance from alien species to wheat by induced translocations. *In* Mutation Breeding for Disease Resistance, Int. Atom. Energy Agency, Vienna:67-77.

MORRISON, J. W. 1954 Chromosome interchange by misdivision in Triticum. Canad. J. Bot. *32*:281-284.

MURAMATSU, M. 1968 Studies on translocations between hairy neck chromosome of rye and chromosomes which belong to homoeologous group 5 of common wheat. Proc. XII Int. Congr. Genet. *1*:180.

OKAMOTO, M., and E. R. SEARS 1962 Chromosomes involved in translocations obtained from haploids of common wheat. Canad. J. Genet. Cytol. *4*:24-30.

QUINN, C. J., and C. J. DRISCOLL 1967 Relationships of the chromosomes of common wheat and related genera. Crop. Sci. *7*:74-75.

RILEY, R., V. CHAPMAN and R. JOHNSON 1968 The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synapsis. Genet. Res., Camb. *12*:199-219.

RILEY, R., and G. KIMBER 1966 The transfer of alien genetic variation to wheat. Rep. Plant Breed. Inst., Camb. 1964-65:6-36.

SEARS, E. R. 1954 The aneuploids of common wheat. Mo. Agr. Exp. Sta. Res. Bul. 572:58 pp.

SEARS, E. R. 1956 The transfer of leaf-rust resistance from Aegilops umbellulata to wheat. Brookh. Symp. Biol. *9*:1-22.

SEARS, E. R. 1958 The aneuploids of common wheat. Proc. 1st Int. Wheat Genet. Symp.:221-228.

SEARS, E. R. 1966a Chromosome mapping with the aid of telocentrics. Proc. 2nd Internat. Wheat Genet. Symp.; Hereditas Suppl. Vol. *2*:370-381.

SEARS, E. R. 1966b Nullisomic-tetrasomic combinations in hexaploid wheat. *In* Chromosome Manipulations and Plant Genetics, 29-45. R. Riley and K. R. Lewis, Eds. Oliver and Boyd, Edinburgh and London.

SEARS, E. R. 1967 Genetic suppression of homoeologous pairing in wheat breeding. Ciencia e Cultura *19*:175-178.

SEARS, E. R. 1969 A translocation that probably arose through union of newly produced telocentric chromosomes. Proc. XI Int. Bot. Congr., Absts., 194.

SHARMA, D., and D. R. KNOTT 1966 The transfer of leaf rust resistance from Agropyron to Triticum by irradiation. Canad. J. Genet. Cytol. *8*:137-143.

STEINITZ-SEARS, L. M. 1966 Somatic instability of telocentric chromosomes in wheat and the nature of the centromere. Genetics *54*:241-248.

WIENHUES, A. 1966 Transfer of rust resistance of Agropyron to wheat by addition, substitution and translocation. Proc. 2nd Int. Wheat Genet. Symp., Hereditas Suppl. Vol. *2*:370-381.

Dr. Sears with a group of participants during the morning recess in front of the Student Union, April 22, 1972.