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The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synapsis

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1. THE OBSTACLE OF THE INCORPORATION OF ALIEN VARIATION

The common wheat of agriculture, *Triticum aestivum*, has been subjected to considerable genetic manipulation by breeders for nearly 100 years. In general this has been remarkably successful in providing steady increases in yields and in minimizing the effects of factors that limit production, such as susceptibility to pests and diseases. This has been achieved by the exploitation of the existing genetic variation of *T. aestivum*, and of the related tetraploid *T. turgidum*, by hybridization and selection.

However, attempts to exploit the useful variation of many species that are closely related phylogenetically to wheat have usually failed because, at meiosis in interspecific hybrids and their derivatives, there is no synapsis and recombination between wheat and alien chromosomes. For this reason attention has been given to lines with single pairs of alien chromosomes added to the full wheat complement or substituted for single wheat pairs (Riley & Kimber, 1966). In addition, lines have been used with induced translocations in which alien chromosome segments, with agriculturally beneficial genetic activities, were transferred to wheat chromosomes (Sears, 1956). However, because the overall phenotypic modifications resulting from such genetic changes are usually too gross and too arbitrary, material of this kind has not been noteably useful in practise. An alternative procedure is needed that allows for the incorporation in wheat of alien segments smaller than the entire chromosome and in which the replacement of wheat by alien segments is not at random. The only way satisfactorily to achieve this is to remove the obstacle to recombination between wheat and alien chromosomes, and the purpose of this paper is fully to describe the means by which this was done in the introduction into wheat of the yellow rust resistance of *Aegilops comosa* (Riley, Chapman & Johnson, 1968).

2. MATERIALS

(i) *Hosts*

All the wheat plants used in this work were derivatives of *Triticum aestivum* emend. Thell, ssp. *vulgare* MacKey variety Chinese Spring ($2n = 6x = 42$). The monosomic and telocentric lines of wheat that were used were those originally isolated in Chinese Spring by E. R. Sears.

The yellow rust resistant parent employed was *Aegilops comosa* Sibth. and

Sm. ($2n = 14$). Another species that was used because of its genetic effects on the specificity of meiotic chromosome synapsis was *Aegilops speltoides* Tausch ($2n = 14$).

(ii) *Pathogens*

Inoculations were carried out using vacuum-dried uredospores of *Puccinia striiformis* Westend. belonging to the wheat-attacking physiologic races 2B, 3/55 (Opal-attacking), 8B, 54 or 60.

3. METHODS

(i) *Cytological*

Meiosis was studied in orcein-Feulgen squashes of pollen mother cells from anthers fixed in acetic-alcohol. Determinations of somatic chromosome constitutions were made from squashes of root-tips pretreated in mono-bromonaphthalene and stained by the Feulgen method.

In describing meiotic pairing configurations the following symbols will be used in the present account, ′ = univalent, ″ = bivalent, ‴ = trivalent.

(ii) *Pathological*

Tests for resistance to *Puccinia striiformis* Westend. were carried out on seedlings using the wheat-attacking races listed below together with the commercial wheat varieties with which they have been particularly associated:

Race	Wheat variety attacked
2B	Cappelle–Desprez
3/55 (Opal-attacking)	Hybrid 46 and Opal
8B	Heine VII
54	Peko
60	Rothwell Perdix

Vacuum-dried or fresh uredospores of a single race were mixed with talc and dusted on on to seedlings at the two-leaf stage. The seedlings were then placed in humidity chambers for 16 h, after which they were allowed to dry slowly. Inoculations were repeated 2 days later with the same race to ensure as complete a coverage as possible.

The reactions were scored between 2 and 3 weeks after inoculation. Almost all reactions were clearcut, being either 00–0 (resistant) or 3–4 (susceptible). A few plants from segregating populations which gave a small amount of sporulation, were classified as reaction class 1, and regarded as resistant. The various rust races were used in different experiments and behaviour of the resistance from *Aegilops comosa* gave the same reaction to all of them.

4. GENETIC STRUCTURE OF WHEAT

T. aestivum is an allohexaploid with the genomic structure AABBDD. In its evolution the A genomes were derived from *Triticum monococcum* ($2n = 14$), the B genomes from *Aegilops speltoides* ($2n = 14$) and the D genomes from *Aegilops*

squarrosa ($2n = 14$) (Riley, 1965). Its complement of twenty-one pairs of chromosomes can be classified into three sets each of seven pairs representing the genomes, and into seven homoeologus groups, each of three pairs, representing chromosomes of similar genetic activities (Sears, 1954, 1966). In every homoeologous group there is one pair in every genome and the relationships between homoeologues is presumed to stem from their origin from the same chromosome of the progenitor of all three ancestral diploids. In the designation of wheat chromosomes a number and a letter are used to indicate respectively the homoeologous group and the genome to which each belongs.

Ae. comosa is genomically MM and the relationships between chromosomes of the M genome and those of all three wheat genomes can be regarded as homoeologous. There is no evidence that any one of the wheat genomes is more closely related to the M genome than are the other two wheat genomes.

5. GENETIC CONTROL OF HOMOEOLOGOUS SYNAPSIS

Normally in *T. aestivum* meiotic synapsis is confined to fully homologous partners. Synapsis between homoeologues is prevented by the activity of what is presumed to be a single locus on the long arm of chromosome 5B (Riley & Chapman, 1958; Riley, 1960; Riley & Kempanna, 1963). In the absence of $5B^L$ homoeologues will synapse and recombine, and it is now known that synapsis between wheat chromosomes and the chromosomes of certain alien species is also prevented by the $5B^L$ activity (Riley & Kempanna, 1963; Riley & Law, 1965). Consequently it appeared that knowledge of the $5B^L$ effect might be exploited to create situations in which useful alien genes could be transferred to wheat chromosomes, by recombination.

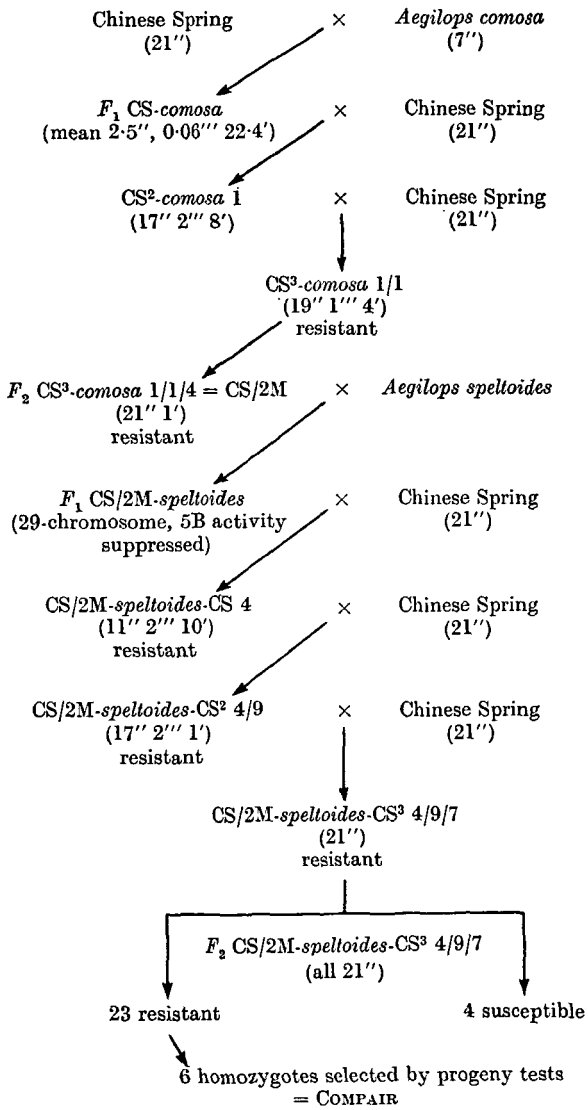
When *T. aestivum* and *Ae. speltoides* are crossed there is homoeologous synapsis in the resulting hybrids, because *Ae. speltoides* carries an allele that is dominant to the $5B^L$ allele that normally prevents such synapsis (Riley & Chapman, 1964, 1966; Kimber, 1966). Clearly, therefore, in attempting to induce homoeologous recombination between an alien chromosome and a wheat chromosome, material can be used that is deficient for $5B^L$ or that incorporates *Ae. speltoides*.

6. ISOLATION OF THE *AEGILOPS COMOSA* CHROMOSOME CAUSING RUST RESISTANCE

In the first part of the breeding programme leading to the isolation of a wheat form with the yellow rust resistance of *Ae. comosa*, an alien chromosome addition line was extracted. This part of the programme, which is illustrated in Text-fig. 1, paralleled and repeated the independent isolation of chromosome 2M of *Ae. comosa* that has already been described by Riley, Chapman & Macer (1966).

T. aestivum Chinese Spring was crossed with *Ae. comosa* to produce 28-chromosome hybrids in which there was no evidence of meiotic synapsis between wheat and *Aegilops* chromosomes. The hybrids were backcrossed to Chinese Spring and among the derivatives was a 48-chromosome plant (CS^2-*comosa* 1) in which the

maximum pairing at meiosis was 17″ 2‴ 8′. This plant, and a number of others consideration of which is irrelevant to the present discussion, were again backcrossed to Chinese Spring.



Text-fig. 1. The pedigree of Compair. (The figures in brackets indicate the maximum chromosome pairing in pollen mother cells using the symbols ′ = univalent, ″ = bivalent, ‴ = trivalent.)

Seedlings in the resulting second backcross generation were tested for their reaction to yellow rust, and a number of individuals with resistance equivalent to *Ae. comosa* was isolated. One of these (CS3-*comosa* 1/1), which was a derivative of CS2-*comosa* 1, had 45 chromosomes and its maximum chromosome pairing at meiosis was 19″ 1‴ 4′. This plant was self-fertile and was allowed to self-pollinate.

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One of its derivatives (CS^3-*comosa* 1/1/4), which was as resistant to yellow rust as *Ae. comosa*, had 43 chromosomes and at meiosis regularly formed 21'' 1' (Plate 2*a*). When this plant was allowed to self-pollinate its derivatives segregated into rust-resistant and rust-susceptible categories. All the susceptibles had 42 chromosomes while the resisters had 43 and 44 chromosomes, consequently the unpaired chromosome of CS^3-*comosa* 1/1/4 was responsible for its disease resistance and had been derived from *Ae. comosa*.

In another line derived in a similar manner a 44-chromosome rust resistant plant was isolated (CS^3-*comosa* 4/17/12) (Riley *et al.* 1966) (Plate 2*b*). The line derived from this plant was shown to have the twenty-one pairs of chromosomes of Chinese Spring and a pair of *Ae. comosa* chromosomes that was responsible for the rust resistance. The chromosome complements of CS^3-*comosa* 1/1/4 and CS^3-*comosa* 4/17/12 were shown to be identical except that the additional alien chromosome—introducing the disease resistance—was disomic in CS^3-*comosa* 4/17/12 but monosomic in CS^3-*comosa* 1/1/4.

Riley *et al.* (1966) showed that, in 43-chromosome plants with monosomic additions of this chromosome to the full wheat complement, the alien chromosome was transmitted to the progeny by approximately 0·50 of the functioning eggs and by about 0·13 of the functioning pollen grains. At first anaphase of meiosis in such monosomic addition plants, the *Ae. comosa* chromosome was a laggard. When the laggard divided into its chromatid halves it was shown to be extremely heterobrachial with one arm about three times the length of the other (Plate 1*a*).

There are two pairs of chromosomes in *Ae. comosa* with this structure (Plate 1*b*) but it is not possible to assert which of these two pairs is responsible for the rust resistance of the addition lines.

7. GENETIC DETERMINATION OF THE HOMOEOLOGY OF THE *AEGILOPS COMOSA* CHROMOSOME

The genetic affinities of this *Ae. comosa* chromosome with chromosomes of the wheat complement were determined by whole chromosome substitution procedures. This involved crossing, as female parents, lines monosomic, in turn, for each chromosome of the complement of Chinese Spring with the 44-chromosome disomic addition line, CS^3-*comosa* 4/17/12. Selection was practised in the F_1 generation for plants with 42 chromosomes and these were confirmed at meiosis to have 20'' 2'. They had, therefore, 20 wheat chromosomes disomic and one wheat chromosome and the *Ae. comosa* chromosome monosomic. There were 21 distinct F_1's of this type, differing from each other in the wheat chromosome that was monosomic.

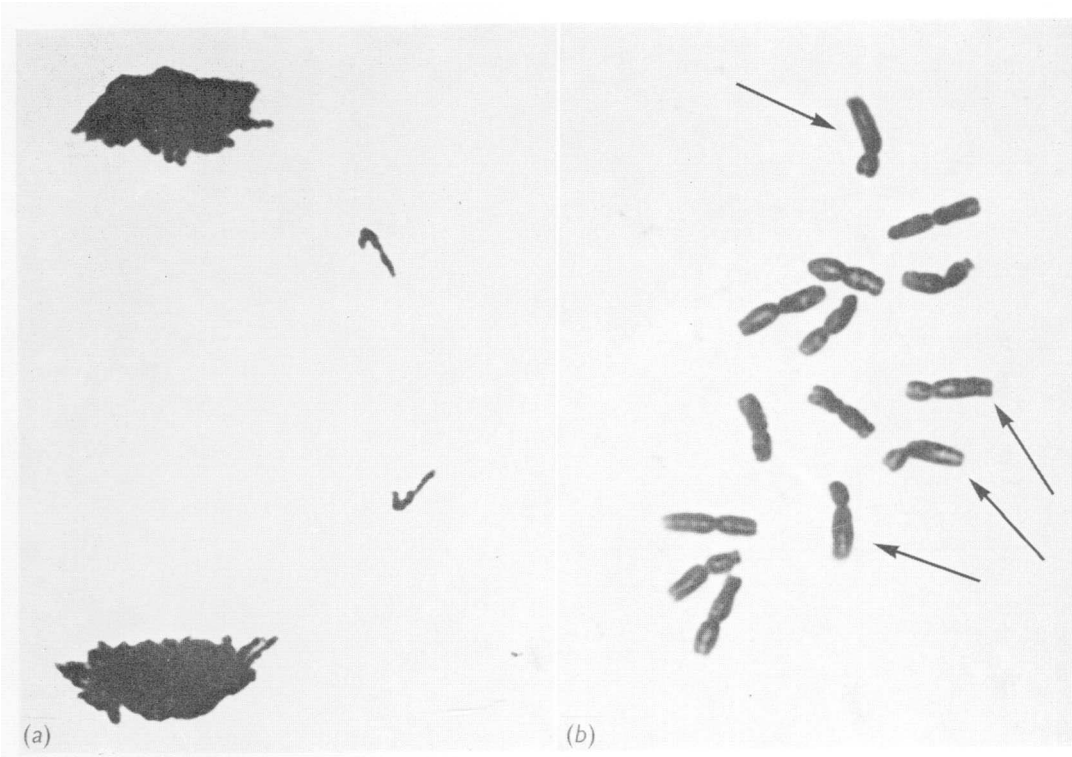
Gametes of the doubly monosomic F_1 plants could receive and transmit either both the wheat and *Aegilops* monosomes, or only one of them or neither. If the wheat monosome was included in 0·25 and excluded from 0·75 gametes—as estimated from the behaviour of wheat monosomics by Sears (1953) and Morrison

(1953), and the *Aegilops* chromosome was transmitted to 0·50 gametes—as estimated by Riley *et al.* (1966), the frequencies of occurrence of gametes of the four constitutions can be predicted. Assuming the independent transmission of the wheat and the *Aegilops* chromosomes, 0·125 gametes would include both, 0·125 only the wheat and 0·375 only the *Aegilops* chromosome, while 0·375 would include neither.

The occurrence of gametes with these constitutions implies that the F_2 generation will segregate into classes with every permutation of from zero to two wheat and from zero to two *Aegilops* chromosomes. The frequencies of each type of F_2 segregant can be predicted from the frequencies of gametes, but the F_2 segregation will be disturbed by the differential competitive ability of pollen grains. In monosomics of wheat and in lines with monosomic additions of alien chromosomes, there is no evidence of differential viability of eggs with different chromosome constitutions. Consequently it can be assumed that, in the doubly monosomic F_1 plants, the proportions of eggs that functioned, with the four possible chromosome constitutions, was not different from the proportions in which they were formed.

It might be expected, however, that pollen grains with different chromosome constitutions would differ in their relative success in fertilization. For example, it is known that, in 41-chromosome monosomics of wheat, although 0·75 pollen grains have 20 chromosomes only 0·04 of the pollen that participates in fertilization has this constitution. There is therefore strong competition against 20-chromosome pollen and similarly strong competition is to be expected against such pollen in the present doubly monosomic F_1's. In addition pollen grains with 20 wheat and one *Aegilops* chromosome can only be expected to function competitively with a frequency corresponding to their proportion in the pollen population when the *Aegilops* chromosome compensates genetically for the defects resulting from the absence of the wheat chromosome. The success of such pollen will therefore indicate a genetic relationship between the wheat chromosome monosomic in the parental genotype and the alien chromosome. Conversely the failure in fertilization of this pollen will demonstrate the absence of such genetic correspondence.

The ability of pollen grains of the four constitutions to participate in fertilization can be determined by scoring the segregation for rust resistance or susceptibility, which indicates the presence or absence of the *Aegilops* chromosome in the F_2's obtained from doubly monosomic F_1's. This was the procedure originally used by Johnson (1966) in studying an *Agropyron* chromosome. Assuming that gametes of the four possible constitutions are formed in the frequencies suggested earlier, and that there is no differential viability of eggs, then the predicted F_2 segregation will change as different categories of pollen are eliminated. If all the pollen is equally competitive, including that with only 20 chromosomes, 0·75 of the progeny will be resistant (Riley *et al.* 1966), whereas if there is equal competitive ability but the 20-chromosome pollen always fails 0·90 will be resistant. By contrast, if neither the 20-chromosome pollen nor the 21-chromosome substitution pollen functions, 0·75 of the progeny will be resistant. Since, on the evidence of the behaviour of wheat monosomics, it is reasonable to assume that 20-chromosome



(*a*) First anaphase of meiosis in a pollen mother cell of a 43-chromosome plant with the monosomic addition, to the full wheat complement, of chromosome 2M of *Ae. comosa*. Chromosome 2M is dividing into its chromatid halves showing its heterobrachial structure. (*b*) The chromosomes of *Ae. comosa* in a root-tip squash after pretreatment with monobromonaphthalene showing the two heterobrachial pairs (arrowed).

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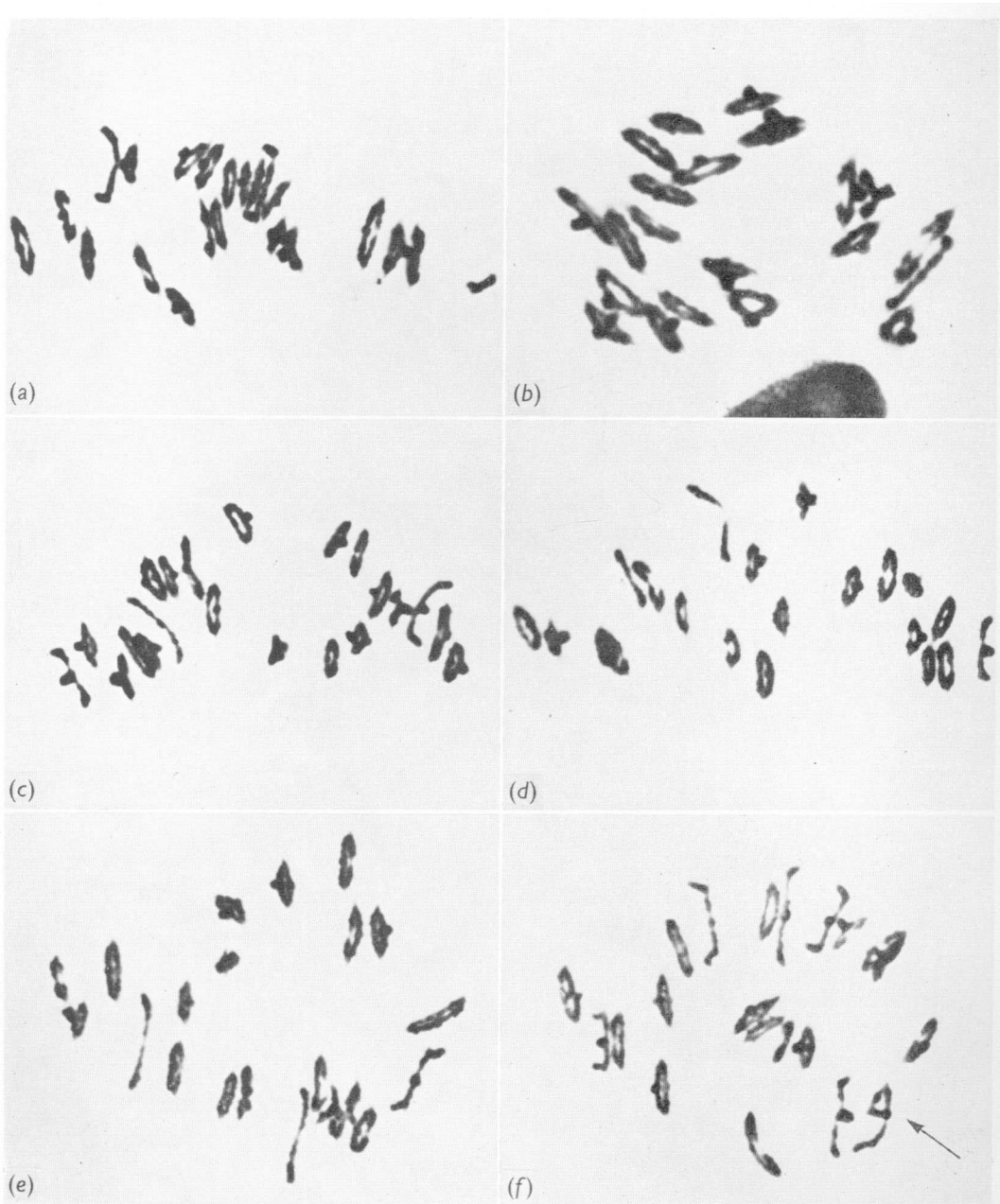

First metaphase of meiosis in pollen mother cells of the following genotypes: (*a*) Monosomic addition of chromosome 2M to the full wheat complement, with 21″ 1′. (*b*) Disomic addition of chromosome 2M to the full wheat complement, with 22″ (two overlying). (*c*) Chinese Spring wheat, with 21″. (*d*) Compair, with 21″. (*e*) Compair × Chinese Spring, with 21″. (*f*) 43-chromosome hybrid from the cross, 2M addition line × Compair, with 20″ 1‴. The panhandle trivalent (arrowed) incorporates chromosome 2M, 2D and 2M/D.

R. RILEY, V. CHAPMAN AND R. JOHNSON

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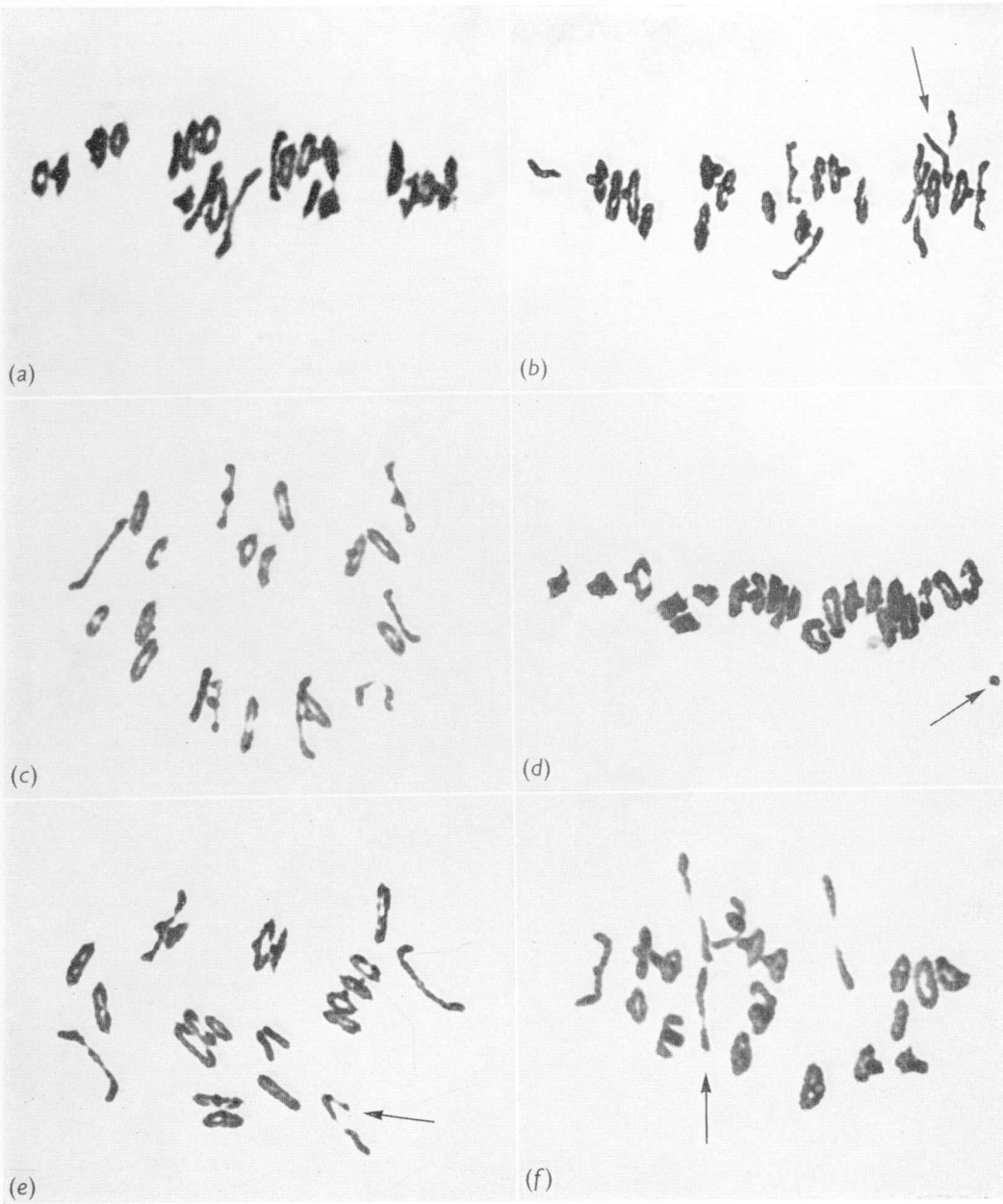

First metaphase of meiosis in pollen mother cells of the following genotypes: (*a*) Line with the disomic substitution of chromosome 2M for chromosome 2D, with 21″. (*b*) 42-chromosome hybrid from the cross, disomic substitution line in which 2M replaces 2B (XIII) × Compair. There are 19″ 1‴ 1′; 2 B (XIII) is the univalent while the trivalent (arrowed) incorporates 2M, 2D and 2M/D. (*c*) 42-chromosome hybrid from the cross, disomic substitution line in which 2M replaces 2D × Compair, with 21″. (*d*) Monosomic addition of the telocentric for the short arm of chromosome 2M to the full wheat complement, with 21″ 1′; the univalent is telocentric $2M^S$ (arrowed). (*e*) 43-chromosome hybrid from the cross $2M^S$ addition line × Compair, with 20″ 1‴. The trivalent (arrowed) incorporates 2D, 2M/D and $2M^S$. (*f*) Compair × Chinese Spring ditelocentric for $2D^R$, with 21″. The grossly heteromorphic bivalent (arrowed) incorporates chromosomes 2M/D and $2D^R$.

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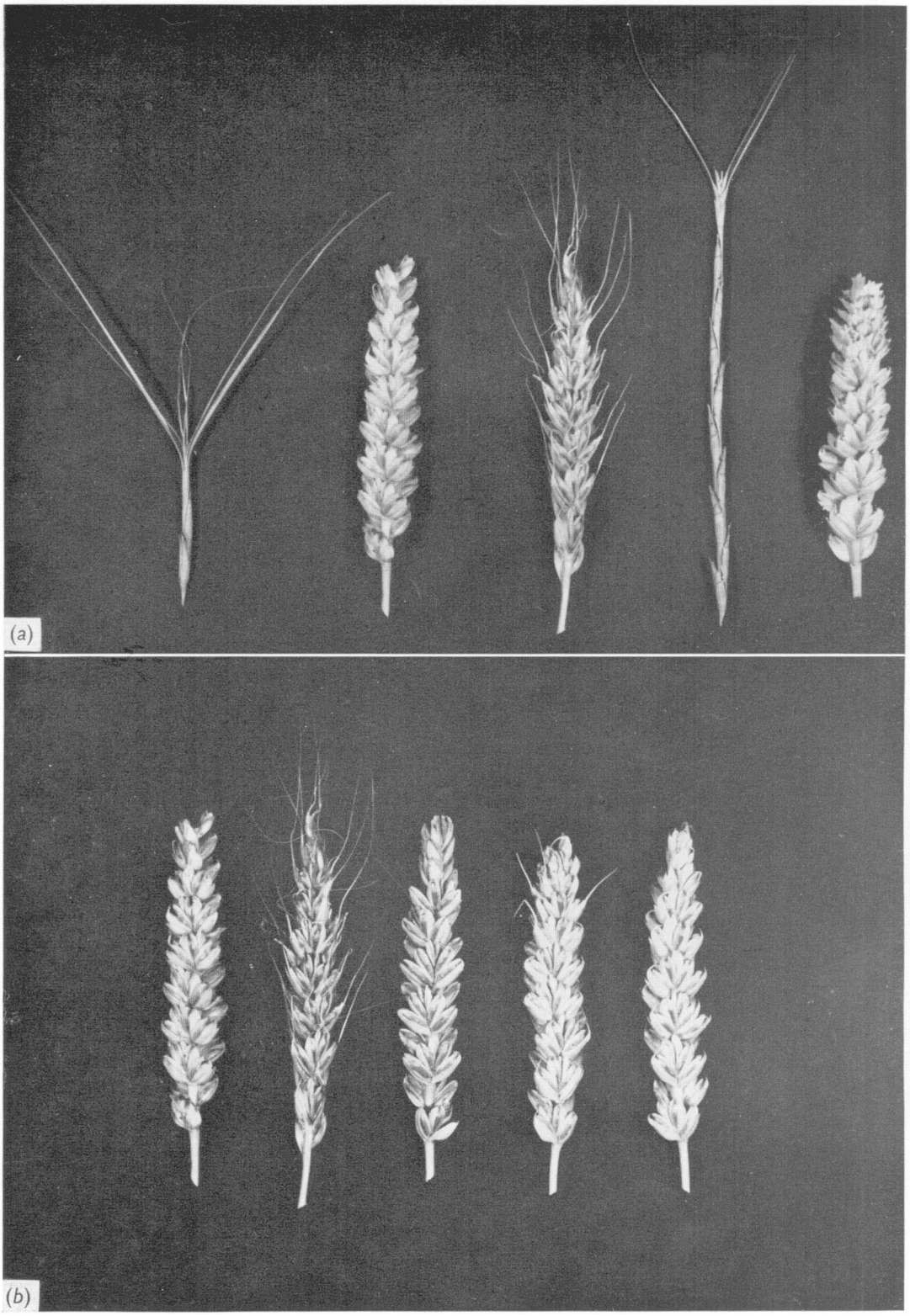

Spikes illustrating the following genotypes: (*a*) from left to right, *Ae. comosa*, *T. aestivum* Chinese Spring, 44-chromosome disomic addition of 2M to Chinese Spring, *Ae. speltoides*, Compair. (*b*) from left to right, Chinese Spring, 2M disomic addition line, and the three 42-chromosome disomic substitution lines 2M for 2 A(II), 2M for 2B (XIII) and 2M for 2D.

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Table 1. *Yellow rust resistance of* F_2 *progenies from 42-chromosome* F_1 *plants, monosomic for a wheat chromosome and the* Aegilops comosa *chromosome, resulting from crosses between wheat parents monosomic for each chromosome, in turn, and the line with the disomic addition of the* Ae. comosa *chromosome giving yellow rust resistance*

Wheat chromosome monosomic	Total plants	Resistant* (%)	Resistant in homoeologous groups (%)
1A	97	57·73	
1A	86	62·79	
1B	71	71·83	66·46
1B	84	69·05	
1D	98	63·27	
1D	27	74·07	
2A (II)	99	87·88	
2A (II)	98	85·71	
2B (XIII)	99	86·87	87·51
2B (XIII)	100	89·00	
2D	100	89·00	
2D	97	86·60	
3A	98	60·20	
3A	94	70·21	
3B	34	61·76	67·01
3B	14	85·71	
3D	81	67·90	
3D	16	56·25	
4A	85	76·47	
4A	43	72·04	
4B	31	51·61	68·11
4B	29	68·97	
4D	77	83·12	
4D	39	56·41	
5A	99	71·72	
5A	72	56·94	
5B	33	66·67	65·86
5B	63	69·84	
5D	102	63·73	
5D	83	66·27	
6A	44	65·91	
6A	68	82·35	
6B	94	68·09	65·02
6B	57	61·40	
6D	65	60·00	
6D	105	52·38	
7A	98	71·43	
7A	89	82·02	
7B	99	54·55	67·32
7B	37	48·65	
7D	98	76·53	
7D	82	70·73	

* Resistant plants had 00–0 reaction types and susceptible plants had 3–4 reaction types.

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pollen will rarely be successful, the distinction between doubly monosomic F_1's with about 90% or about 75% of their progenies resistant will represent a difference in the capacity of the *Aegilops* chromosome to substitute for the wheat chromosomes concerned.

To test chromosome relationships in this way seedlings of the F_2 generation, derived from two hybrids, monosomic for each wheat chromosome in turn and for the *Ae. comosa* chromosome, were inoculated with yellow rust. The controls for this test were fourteen seedlings of *Ae. comosa* and 100 seedlings of the disomic addition line CS^3-*comosa* 4/17/12 all of which give 00–0, resistant, reactions. By contrast 187 seedlings of Chinese Spring all gave 3–4, susceptible, reactions. The results of the test of the F_2 derivatives were very striking in showing a distinctly higher frequency of resistance in all the progenies from parents in which chromosomes of homoeologous group 2 had been monosomic (Table 1). No other progeny had a frequency of resistant plants exceeding that in the group 2 progenies, and in the group as a whole 87·51% were resistant compared with 68·11% in group 4, the next highest group.

Table 2. *Analysis of variance of the percentages, converted to angles, of rust resistant plants in the* F_2 *progenies from* F_1 *plants monosomic for the* Aegilops comosa *chromosome and for each wheat chromosome in turn*

	Mean square	Degrees of freedom	Variance ratio†
Genomes	16·42	2	< 1
Homoeologous groups	180·44	6	3·86*
Homoeologous group 2	1045·85	1	22·40**
Other groups	7·35	5	< 1
Genomes-groups	46·70	12	
Error	2·68	21	

† Comparisons were made with the Genomes-groups interaction item since it was significant when compared with the error item.

* P between 0·05 and 0·01.

** $P < 0·001$.

To test the significance of these data the percentage of resistant plants in each of the 42 F_2's was converted to angles and an analysis of variance carried out on the converted data (Table 2). Tests for significance were made against the genome-group interaction item since this was significant relative to the error item (V.R. = 22·82, $P < 0·001$). There were significant differences between homoeologous groups but none between genomes. Homoeologous group 2 was significantly different from the remaining groups but there were no other significant between-group differences.

From the higher frequency of disease-resistant offspring in the group 2 class it seems reasonable to infer that the *Ae. comosa* chromosome was able to compensate genetically in the pollen for the deficiency of group 2 chromosomes but not for the deficiency of any other chromosome. The frequency of 90% resistant

offspring expected on the basis of perfect compensation in the pollen, was not quite attained in group 2, nor was the frequency of 75% resistant in the non-compensating combinations. This may have been due to the occasional success of 20-chromosome pollen or to the diminished competitive ability of 22-chromosome pollen carrying the *Aegilops* chromosome.

A check of the capacity of the *Ae. comosa* chromosome to substitute, with good genetic compensation, for the absence of homoeologous group 2 chromosomes was made by examining meiosis in rust-resistant F_2 plants. This showed that in the derivatives of F_1's in which chromosomes 2A (II), 2B (XIII) and 2D, had been monosomic there were resistant plants with 21″ and with 20″ 1′ (Table 3).

Table 3. *Chromosome constitution of random samples of rust-resistant* F_2 *plants in the progenies of* F_1 *plants in which chromosomes of homoeologous groups 2 and 7 were monosomic*

Wheat chromosome monosomic	Total	Monosomic substitution 20″ 1′	Disomic substitution 21″	F_1 repeat 20″ 2′	Monosomic addition 21″ 1′	Disomic addition 22″
2A (II)	67	23	5	21	18	—
2B (XIII)	44	15	2	16	10	1
2D	41	14	5	12	10	—
Group 2 total	152	52	12	49	38	1
7A	19	—	—	10	9	—
7B	21	—	—	10	10	1
7D	23	—	—	13	9	1
Group 7 total	63	—	—	33	28	2

There were no resistant F_2 plants with these constitutions in the control plants derived from F_1's in which chromosomes of homoeologous group 7 had been monosomic. Plants with these constitutions in the group 2 categories were shown to carry 20 pairs of wheat chromosomes and the *Ae. comosa* chromosome, either disomic or monosomic, substituted for the wheat chromosome that had been monosomic in the F_1's. This confirmed that the genetic relationships are such that substitution pollen was capable of functioning with good competitive ability because the *Aegilops* chromosome compensated for the defects resulting from the deficiency of the wheat chromosome. Moreover, the disomic and monosomic substitution plants were of relatively normal phenotype and fertility—again confirming the capacity of the *Ae. comosa* chromosome to substitute for 2A (II), 2B (XIII) and 2D. Lines with disomic substitution of the *Ae. comosa* chromosome for these three wheat chromosomes were established from this test, and these lines were used in subsequent analyses.

Taken together the present evidence demonstrates the close genetic affinity of the *Ae. comosa* chromosome to the chromosomes of wheat homoeologous group 2, and indeed it is sufficient to show that the *Aegilops* chromosome belongs to this homoeologous group. Consequently, because *Ae. comosa* carries the M genome,

the chromosome causing yellow rust resistance can be designated 2M (Riley *et al.* 1966).

Although chromosome 2M is closely similar in genetic activity and presumably in DNA structure to its wheat homoeologues, in its isolation as an addition line its integrity had been maintained through three meiotic divisions in the presence of these homoeologues. Consequently, at least when chromosome 5B is active, there is no synapsis or recombination with its homoeologues. However, it seemed that, if the 5B activity were inhibited, homoeologous recombination might occur and in this way the gene, presumed to be responsible for yellow rust resistance, might be incorporated in a wheat chromosome. The next part of the breeding programme was carried out with the aim of inducing 2M to recombine homoeologously.

8. GENETIC INTERFERENCE WITH THE 5B SYSTEM

In order to induce homoeologous recombination the 43-chromosome plant, CS^3-*comosa* 1/1/4, which was monosomic for chromosome 2M, was crossed with *Ae. speltoides* (Text-fig. 1). Hybrids were selected that had 29 chromosomes and in which chromosome 2M was present in addition to seven chromosomes of *Ae. speltoides* and 21 chromosomes of Chinese Spring. In these hybrids, because of the presence of the dominant allele introduced from *Ae. speltoides*, the normal activity of chromosome 5B of wheat was suppressed and homoeologous synapsis took place. Operationally the object was to create a situation in which chromosome 2M could synapse and recombine with its wheat homoeologues so that the 2M segment, determining rust resistance, could be transferred to a wheat chromosome. In this way it was anticipated that the *Ae. comosa* resistance might be incorporated in a wheat genotype that was modified less drastically than when the entire 2M chromosome is substituted for a wheat homoeologue.

The intention was to return to the modified wheat genotype by backcrossing, using Chinese Spring as the recurrent parent, but this of course required unequivocal recognition of the presence of the rust resistance resulting from the activity of chromosome 2M. Initially it was thought that confusion might be caused by the rust resistance of *Ae. speltoides*, because when twenty seedlings of this species were inoculated with yellow rust they all gave 00–0, resistant, reaction. However, when 10 F_1 seedlings of the cross *T. aestivum* Chinese Spring × *Ae. speltoides* were inoculated with yellow rust they all gave 3–4, susceptible, reactions. Consequently the resistance of *Ae. speltoides* is recessive to the susceptibility of Chinese Spring. In a backcrossing programme, therefore, the resistance caused by 2M, which had already been shown to be dominant, would be recognizable and never confused with the recessive resistance of *Ae. speltoides*.

The 29-chromosome hybrids (CS/2M-*speltoides*) were backcrossed with *T. aestivum* Chinese Spring and the derivatives of the cross tested for resistance to yellow rust. Among other resistant plants, discussion of which is irrelevant to the present account, there was one (CS/2M-*speltoides*-CS 4) with 38 chromosomes. The maximum pairing at meiosis in this plant was 11″ 2‴ 10′ and it was self-sterile and was backcrossed with Chinese Spring.

The derivatives of this backcross were inoculated with yellow rust and resistant plants were selected. One of these (CS/2M-*speltoides*-CS^2 4/9) had 41 chromosomes and at meiosis formed 17″ 2‴ 1′. This plant was backcrossed with Chinese Spring and the derivatives tested for rust resistance.

One resistant derivative (CS/2M-*speltoides*-CS^3 4/9/7) had 42 chromosomes and regularly formed 21″ at meiosis. As it was of comparatively normal phenotype and was fully self-fertile, further backcrossing to Chinese Spring was abandoned. Twenty-seven seedlings, grown from seeds obtained by self-pollination, were inoculated with yellow rust and segregated to give 23 resistant: 4 susceptible. Apparently CS/2M-*speltoides*-CS^3 4/9/7 had been heterozygous, as was to be expected since it was a backcross product, and on a segregational definition carried dominant and recessive alleles at a locus affecting rust resistance.

Progenies obtained by self-pollination of the resistant plants in the F_2 of CS/2M-*speltoides*-CS^3 4/9/7 were tested for rust resistance and those with no susceptible segregants were selected. In this way stocks homozygous for the *Ae. comosa* rust resistance were isolated and were examined at maturity for segregation for gross morphological characters. Since there was no marked segregation all were retained, and although the separate families were individually identified, for further work and for distribution, they were regarded as being identical so far as the status of their rust resistance is concerned.

In addition, rust-resistant plants in the F_2 of CS/2M-*speltoides*-CS^3 4/9/7 were crossed with standard plants of *T. aestivum* Chinese Spring. At meiosis in the resulting hybrids 21″ were regularly formed so that the derivatives of the backcrossing programmes, while displaying the rust resistance previously associated with the presence of chromosome 2M of *Ae. comosa*, also carried 21 pairs of chromosomes that were in turn homologous, at least in part, with the 21 chromosomes of wheat. Apparently, therefore, recombination had taken place between chromosome 2M and a wheat chromosome, and a form of *T. aestivum* had been isolated that displayed the rust resistance of *Ae. comosa*. The homozygous rust-resistant stocks isolated from CS/2M-*speltoides*-CS^3 4/9/7 were given the varietal name 'Compair' and for convenience in the succeeding discussion this name will be used.

9. ANALYSIS OF COMPAIR

(i) *Recognition of the modified chromosome*

A cytogenic analysis of Compair was carried out in order to evaluate its potential as a parent in future wheat breeding programmes and to determine the kind of homoeologous recombination that had occurred between a wheat and an alien chromosome following interference with the 5B system. As a first step the first metaphase of meiosis was examined in Chinese Spring × Compair hybrids and in the two parents (Table 4). The regularity of pairing in the hybrids was only slightly less than in the parents, more than 75% of cells having 21 bivalents (Plate 2*c*, *d*, *e*). Clearly, therefore, all 21 chromosomes of Compair have homologues in Chinese Spring.

Next, hybrids were studied from crosses involving the 44-chromosome line, with chromosome 2M added disomically to the intact chromosome complement of Chinese Spring. This line was crossed with Chinese Spring and Compair and the meiotic behaviour was examined in the two types of 43-chromosome hybrids produced (Table 5). Whereas in the 2M addition line × Chinese Spring hybrids the monosomic chromosome 2M was always a univalent, in 2M addition line × Compair hybrids there was a trivalent in which chromosome 2M was involved in 90% of cells. Clearly Compair carried a chromosome that is homologous, at least in part, with chromosome 2M and is also homologous, at least in part, with a standard chromosome of Chinese Spring. Since the trivalent was almost always a chain, the chromosomes involved must have been arranged 2M—2M/Chinese Spring—Chinese Spring. Panhandle trivalents (⌓) were also rarely observed but consideration of their significance will be deferred until later (Plate 2*f*).

Table 4. *Mean chromosome pairing at first metaphase of meiosis in* Triticum aestivum *Chinese Spring and Compair and the* F_1 *hybrid between them. The range for each configuration in brackets (thirty cells per genotype)*

Genotype	Univalents	Bivalents	
		Closed	Total
Chinese Spring	0·07 (0–2)	19·20 (17–21)	20·97 (20–21)
Compair	0·27 (0–2)	18·37 (12–21)	20·87 (20–21)
Chinese Spring × Compair	0·47 (0–2)	18·03 (15–20)	20·77 (20–21)

Consideration was then given to hybrids derived from the three 42-chromosome lines in which chromosome 2M was substituted disomically for chromosome 2A (II), 2B (XIII) and 2D, of Chinese Spring in turn (Plate 3*a*). All of these lines were crossed with Compair and meiosis was examined in the resulting hybrids (Table 5). In the crosses 2M/2A (II) substitution line × Compair and 2M/2B (XIII) substitution line × Compair, a trivalent and a univalent were present in at least half the cells and there was no cell without a univalent (Plate 3*b*). These hybrids therefore carried the distinctive Compair chromosome and its partial homologues, chromosome 2M and an unknown wheat chromosome, while the constant univalent was either chromosome 2A (II) or 2B (XIII) contributed by the Compair parent but not by the substitution lines.

By contrast, in the 2M/2D substitution line × Compair, there was never a trivalent and 86% of the cells scored had 21 bivalents (Plate 3*c*). The absence of a univalent in most cells implies that chromosome 2D of Compair carries a segment that is homologous with chromosome 2M. However, a segment of 2D must be retained to give rise to trivalent formation in the hybrids described previously. Consequently it can be concluded that homoeologous recombination occurred in the development of Compair between chromosomes 2M and 2D.

This diagnosis was confirmed by a monosomic analysis of the inheritance of rust resistance. The three lines of Chinese Spring monosomic in turn for chromosome 2A (II), 2B (XIII) and 2D, were pollinated by Compair. The resulting hybrids were checked at meiosis and monosomics with 20″ 1′ were selected. Seedlings of the F_2 generation derived from monosomic F_1's were inoculated with yellow rust and scored for resistance or susceptibility (Table 6). The progenies

Table 5. *Mean chromosome pairing at first metaphase of meiosis in* F_1 *hybrids between Chinese Spring, Compair and lines based on Chinese Spring with additions or substitutions of chromosome 2M. The range for each configuration in brackets (thirty cells per genotype)*

Genotype	Chromosome number	Univalents	Bivalents		Trivalents
			Closed	Total	
2M addn. × Chinese Spring	43	1·07 (1–3)	18·60 (17–21)	20·93 (20–21)	—
2M addn. × Compair	43	0·37 (0–2)	16·23 (11–19)	19·97 (19–21)	0·90 (0–1)
2M/2A (II) subst. × Compair	42	1·67 (1–3)	15·67 (11–20)	19·37 (18–20)	0·53 (0–1)
2M/2B (XIII) subst. × Compair	42	1·70 (1–4)	16·80 (14–19)	19·40 (18–20)	0·50 (0–1)
2M/2D subst. × Compair	42	0·27 (0–2)	18·90 (17–21)	20·87 (20–21)	—

Table 6. *Segregation of rust resistance and susceptibility in the* F_2 *generation from hybrids between Chinese Spring and Compair monosomic for chromosome 2A (II), 2B (XIII) or 2D*

Cross	Total F_2 plants	Resistant			Susceptible	χ^2 for 3 resist.: 1 suscept.
		00–0	1	Total	3–4	
Monosomic 2A (II) × Compair	87	63	3	66	21	0·034
Monosomic 2B (XIII) × Compair	91	67	4	71	20	0·43
Monosomic 2D × Compair	91	75	12	87	4†	20·60**

† These 4 plants all had 40 chromosomes.
** Significant at $P = 0·001$.

obtained from F_1 plants in which chromosomes 2A (II) and 2B (XIII) had been monosomic segregated to give ratios that were not significantly different from 3 resistant: 1 susceptible. By contrast there was a pronounced deviation from a 3:1 ratio in the progeny from the F_1 monosomic for chromosome 2D. This is the characteristic result expected when the location of a dominant allele is determined by monosomic analysis. It arises from the strong competitive advantage of 21-chromosome pollen which must carry the monosomic chromosome, so that when the marker is on this chromosome it is transmitted to the majority of the progeny. The chromosome constitutions of the susceptible seedlings in the monosomic 2D progeny were determined and all proved to be nullisomic. Where the

chromosome carrying the dominant marker gene is deficient the recessive phenotype must be expressed, so that this result accords with expectation.

Both genetic and cytogenetic examinations of Compair agree in showing that chromosome 2D is changed from its condition in Chinese Spring. Genetically it is responsible for the determination of yellow rust resistance and cytologically it carries a segment of *Ae. comosa* chromosome 2M. Of course it is reasonable to assume that an activity of the 2M segment, introduced by homoeologous recombination, causes the rust resistance. In the discussion that follows the modified chromosome will be designated 2M/D.

(ii) *The structure of chromosome 2M/D*

In order to ascertain the structure of the modified chromosome 2M/D, use was made of lines with relevant chromosomes marked by telocentric conditions. One of these had a telocentric derived from 2M which, as has been mentioned earlier, is a markedly heterobrachial chromosome. This telocentric was isolated in a member of a progeny of a 43-chromosome line that carries 2M as a monosomic addition to the full complement of Chinese Spring (Plate 3*d*). Initially the telocentric, which was for the short arm of 2M, was obtained in the monosomic condition in a 43-chromosome plant, but among its derivatives were 44-chromosome ditelocentric additions. When inoculated with yellow rust this $2M^S$ addition line was fully susceptible, giving 3–4 reaction scores. From this it can be concluded that the rust resistance caused by 2M results from an activity of the long arm.

Table 7. *Mean chromosome pairing at first metaphase of meiosis in* F_1 *hybrids between Chinese Spring and Compair and the line of Chinese Spring carrying the telocentric* $2M^S$ *as an addition to the normal complement. The range of each configuration in brackets* (*thirty cells per genotype*)

Genotype $2M^S$ addn. ×	Chrom. number	Univalents	Bivalents		Trivalents	$2M^S$ behaviour
			Closed	Total		
Chinese Spring	43	1·33 (1–5)	18·93 (16–21)	20·83 (19–21)	—	Univalent in every cell
Compair	43	1·00 (0–3)	18·00 (13–20)	20·30 (19–21)	0·47 (0–1)	Present in all trivalents but never in bivalent

The $2M^S$ addition line was crossed with Chinese Spring and with Compair. When the resulting 43-chromosome hybrids were examined at meiosis, $2M^S$ was a univalent in every cell of those from the cross $2M^S$ addition line × Chinese Spring (Table 7). However, in the $2M^S$ addition line × Compair hybrids, there was a trivalent which involved $2M^S$ in nearly half the cells (Plate 3*e*) and where the telocentric was not in a trivalent it was a univalent. Consequently chromosome 2M/D has sufficient of the short arm of 2M to ensure a considerable amount of synapsis.

A further test involved the use of the lines of Chinese Spring in which in turn chromosomes 2A (II), 2B (XIII) and 2D were ditelocentric. Each of these lines was used to pollinate Compair and the resulting 42-chromosome hybrids had one chromosome marked by a telocentric condition. At meiosis the 2A $(II)^S$ and 2B $(XIII)^L$ telocentric paired regularly in bivalents with their homologues (Table 8). Chromosome 2D is too nearly isobrachial for the long and short arms to be distinguished readily so that the 2D telocentric that is present in the stock used in the present work is known as the right arm ($2D^R$). In the Compair × Chinese Spring ditelocentric $2D^R$ hybrids the telocentric paired frequently with chromosome 2M/D (Plate 3*f*). Consequently it can be concluded that chromosome 2M/D incorporates a sufficient segment of the right arm of chromosome 2D to ensure synapsis in most cells.

Table 8. *Mean chromosome pairing at first metaphase of meiosis in* F_1 *hybrids between Compair and lines of Chinese Spring ditelocentric for every chromosome of homoeologous group 2 in turn. The range of each configuration in brackets (thirty cells per genotype)*

Genotype	Chromosome number	Univalents	Bivalents		Cells with telo. bivalent (%)
			Closed	Total	
Compair × ditelocentric 2A $(II)^S$	42	0·40 (0–2)	15·07 (13–18)	20·80 (19–21)	97
Compair × ditelocentric 2B $(XIII)^L$	42	0·60 (0–2)	15·73 (11–18)	20·70 (20–21)	100
Compair × ditelocentric $2D^R$	42	0·40 (0–2)	16·97 (15–20)	20·80 (20–21)	87

It has previously been pointed out that the rust resistance caused by 2M depends upon an activity of the long arm. Consequently chromosome 2M/D must incorporate a segment of the long arm of 2M. From the present evidence therefore it can be concluded that in the origin of chromosome 2M/D recombination took place in the long arm of 2M and the right arm of 2D. The structure of 2M/D must therefore be such that it incorporates the entire short arm, the centromere and a proximal segment including the region responsible for rust resistance of the long arm of 2M, and a distal segment of the right arm of 2D.

Further evidence that the structure of 2M/D is as just described came from the occurrence of panhandle (⌒) trivalents in the 43-chromosome hybrids from the cross, 2M addition line × Compair. For the occurrence of this configuration, chiasma formation must have occurred between chromosome 2M and 2M/D on both sides of the centromere, and between 2M/D and 2D at a point distal to one of the 2M-2M/D chiasmata. Moreover, in hybrids from the cross of Compair with the 42-chromosome substitution line in which chromosome 2M replaced chromosome 2D, 21 bivalents with chiasmata on both sides of the centromere were formed in seven per cent of the cells scored (Table 5). This also implies that 2M/D must carry 2M material on both sides of the centromere. In the hybrid

Chinese Spring × Compair there was always at least one open bivalent in which chiasma formation had taken place on only one side of the centromere (Table 4). This also agrees with the postulated structure of 2M/D, since in a 2M/D-2D bivalent homologous segments would only be present on one side of the centromere.

10. THE 2M–2D RECOMBINATION

From the analysis of Compair a fairly clear picture emerges of the structure of chromosome 2M/D and we can thus visualise the process by which it arose. Normally, when chromosome 2M is isolated in a wheat background it does not synapse with its wheat homoeologues but apparently it was possible for synapsis to take place when the 2M addition line was hybridized with *Ae. speltoides*. The present work constitutes the first cytogenetical evidence that the *Ae. speltoides* genotype suppresses the 5B activity, but purely cytological evidence of this has been reported earlier (Riley & Chapman, 1964, 1966; Johnson & Kimber, 1967).

Recombination between 2M and 2D could have occurred either in the initial 29-chromosome hybrid involving *Ae. speltoides* or in one of the backcross generations derived from this hybrid. Homoeologous recombination could have occurred in any backcross progeny that had received the dominant allele of *Ae. speltoides* which suppresses the 5B activity. Interference with the 5B activity by the introduction of the *Ae. speltoides* dominant thus offered the potentiality of protracting the number of generations in which homoeologous recombination could occur. A reversion to the normal condition, with synapsis restricted to full homologues, would not take place until the *Ae. speltoides* dominant was displaced during the backcrossing programme. This has clearly happened in Compair since pairing is restricted to homologues.

Whether in the initial hybrid or in a subsequent generation, chromosomes 2M and 2D apparently synapsed in such a way that there was recombination in the long arm of 2M and the right arm of 2D. This raises the problem of the nature of the discrepancy of arm ratios in these two homoeologues. Since the primitive chromosome structure in the *Triticum–Aegilops* group is with median centromeres, chromosome 2D must be evolutionarily primitive and chromosome 2M, with a distally placed centromere, must be derived. The genetic evidence for the homoeology of 2M to group 2 is strong, so it is unlikely that the distal position of its centromere resulted from translocation or deletion. The most likely structual change that could have altered the centromere position so drastically, without a modification of genetic activity, is pericentric inversion.

If chromosome 2M carries a pericentric inversion relative to 2D, the regions in which recombination could occur to give a balanced product would be confined to the distal segments outside the proximal inversion. Recombination within the inverted segment would lead to the production of unbalanced recombinant chromosomes with duplications and deficiences. Such unbalanced recombinants might well be inviable and selected against. Moreover, if the region of 2M responsible for rust resistance is either within the inverted segment or outside the

inverted segment but closely linked to it, the only single recombinant products, with a segment of 2D and a segment of 2M with the rust resistance-causing region, would necessarily be of the general structure of 2M/D, carrying part of $2M^L$, the 2M centromere and $2M^S$.

Unfortunately there is no way of determining the extent of the $2D^R$ segment in 2M/D, although it is obviously large enough to ensure regular synapsis with 2D. For the purpose of wheat improvement the smaller the segment of 2M remaining after recombination the better, but the structure of 2M may limit the extent to which its contribution can be reduced. The significant aspect of the present result is the unequivocal demonstration that genetic interference with the 5B activity can be exploited to induce homoeologous recombination between wheat and alien chromosomes. The exploitation of this procedure is not only useful in improving the genotype of the wheat crop but also provides further information on chromosomal relationships, allowing the recognition of homoeology and of the arm equivalence of homoeologues.

11. DESCRIPTION OF COMPAIR AND ITS USE IN BREEDING

(i) *Disease resistance*

Chinese Spring has no seedling resistance to the yellow rust fungus, *Puccinia striiformis*, but even in heavy field epidemics it is never severely infected as a mature plant. By contrast Compair has outstanding seedling resistance which is maintained throughout its life cycle. This resistance, which is expressed as hypersensitive flecking, is effective against all the physiologic races to which Compair has been exposed including 2B, 3/55 (Opal attacking), 8B, 54 and 60.

The resistance segregates in hybrids between Compair and Chinese Spring as though conditioned by the dominant allele at a single locus and in conformity with the convention adopted for the designation of yellow rust resistance alleles (Macer, 1966) it has been designated Yr_8. Of course the recognition of Yr_8 depends entirely upon a segregational definition: there is no evidence that a single region of the $2M^L$ segment in chromosome 2M/D is responsible for the effect although this is the simplest hypothesis.

In the introduction of Yr_8 into wheat genotypes adapted to agronomic exploitation, there should be no problem in following its segregation in hybridization programmes. Its presence can be readily scored and the resistance can be treated in the same way as any character determined by a major gene indigenous to the wheat genotype.

(ii) *Phenotype*

Compair is closely similar to Chinese Spring in gross plant morphology, and in its growth rate and time to maturity. It differs from Chinese Spring in having somewhat longer florets, glumes and grains (Plate 4). These are attributes in which the disomic addition line—with chromosome 2M added to Chinese Spring—differs from Chinese Spring, so it may be that they result from the activity of the 2M segment in chromosome 2M/D. There is no reason to suppose that these

characteristics will detract from the usefulness of Compair in wheat improvement programmes but it will be some time before this view can be confirmed.

In the spikes of Chinese Spring the apex of each lemma is prolonged to form an extended tooth or short awn. Compair is developmentally unstable in this character; many spikes are like those of Chinese Spring but others have fully developed awns. This variation in awn development is sometimes found on different spikes of the same plant. It seems likely that the capacity to develop awns is due to the presence of the 2M/D chromosome because homoeologous group 2 chromosomes of wheat are known to promote awn development (Sears, 1954). Indeed group 2 tetrasomics of Chinese Spring have increased awn development and the 44-chromosome addition line disomic for chromosome 2M is also fully awned (Plate 4).

(iii) *Use of Compair in breeding*

The easy use of Compair as a parent in wheat breeding programmes requires that there shall be regular genetic segregation and this, of course, depends upon regular chromosome pairing at meiosis. In order to assess its usefulness, therefore, meiosis was examined in hybrids between Compair and two high yielding varieties, Rothwell Perdix and Maris Ranger, adapted to British agricultural conditions. Both varieties proved to differ from Compair by a single interchange difference, but, apart from the multivalent resulting from interchange heterozygosity, meiosis was quite regular. Every chromosome was paired in 88 per cent of meiotic cells in the Compair × Rothwell Perdix hybrids (Table 9). In 66% of cells in the Compair × Maris Ranger hybrids pairing was regular, and in 4% of those with univalents only one univalent was present and this was due to the failure of pairing of one of the chromosomes involved in the interchange difference.

Table 9. *Mean chromosome pairing at first metaphase of meiosis in* F_1 *hybrids between Compair and Rothwell Perdix and Maris Ranger. The range of each configuration in brackets* (*sixty cells per genotype*)

Genotype Compair ×	Univalents	Bivalents		Trivalents	Quadrivalents	Cells without univalents (%)
		Closed	Total			
Rothwell Perdix	0·27 (0–4)	16·90 (12–20)	20·60 (18–21)	—	0·14 (0–1)	88
Maris Ranger	0·79 (0–6)	15·62 (13–20)	19·48 (17–21)	0·08 (0–1)	0·50 (0–1)	66

From this it can be concluded that in intervarietal hybrids chromosome 2M/D usually pairs with chromosome 2D. The segregation of Yr_8 will consequently be quite regular and breeders can employ Compair without reference to meiotic chromosome behaviour. That is to say, so far as wheat hybridization programmes are concerned, Compair can be treated like any other varietal parent.

12. DISCUSSION

(i) *5B activity in Compair hybrids*

An intriguing insight into the means by which the 5B activity regulates homologous and homoeologous synapsis in wheat is afforded by the behaviour of chromosome 2M/D in hybrids involving Compair. First it should be emphasized that in Compair the meiotic regime has returned to that of Chinese Spring: synapsis is confined to full homologues and there is no homoeologous pairing. In hybrids such as Chinese Spring × Compair (Table 4), or Compair × Rothwell Perdix or Maris Ranger (Table 9) or the 2M/2D substitution line × Compair (Table 5) chromosome 2M/D is present with either 2D or 2M. Under these conditions, on the evidence of chiasma formation, synapsis apparently only takes place between the strictly homologous regions and never between the linked homoeologous regions.

If the normal restriction of synapsis to full homologues in the presence of $5B^L$ results from the relative spatial ordering of homologues and homoeologues, as suggested by Feldman (1966), the present evidence implies that the position of each chromosomal region is autonomously determined. Even if this were so, it might have been anticipated that the linkage of homoeologus to homologous regions would have, at least to some degree, broken down the isolation of homoeologues. Homoeologous segments should have been brought into proximity mechanically, in the train of the homologous segments. The failure of the hemizygous homoeologous segments to synapse must raise some doubt about the general validity of the spatial hypothesis.

(ii) *The use of alien genetic variation in wheat improvement*

The origin of chromosome 2M/D provides unequivocal confirmation that homoeologous recombination between wheat and alien chromosomes results from the suppression of the 5B activity by the genotypes of *Ae. speltoides*. The use of *Ae. speltoides* to induce homoeologous recombination is therefore a valuable and effective means of transferring alien genetic variation to wheat. As an alternative to *Ae. speltoides* another diploid species, *A. mutica*, which similarly promotes homoeologous pairing could be used (Riley, 1966). Homoeologous recombination can also be induced by the development of genotypes carrying an alien chromosome but deficient for chromosome 5B. For this purpose use can be made of lines monosomic for 5B or of the line simultaneously nullisomic for 5B and tetrasomic for a homoeologue. However, a worthwhile advantage is offered by the employment of *Ae. speltoides*. This results from the dominant suppression of the 5B activity which may be retained in some of the backcross generations, thus increasing the probability of appropriate homoeologous recombination occurring.

Using these procedures there is no reason why Yr_8 should not be transferred to any group 2 homoeologue. If Yr_8 were obtained either on chromosome 2A (II) or 2B (XIII) it might then be possible, if restricted 2M segments were present, to duplicate the locus in a wheat background by combining independently isolated

lines. It should soon be possible to determine whether this procedure is feasible and profitable.

Finally, mention should be made of the general significance of the present results for wheat improvement. For the first time practical use has been made of knowledge of the ways in which it is possible to manipulate the genetic regulation of synapsis in the wheat group. The isolation of Compair demonstrates that the range of natural variation available for wheat improvement is no longer confined to tetraploid and hexaploid forms of *Triticum* but extends to many wild species related to *T. aestivum*. Henceforward it is to be expected that the incorporation of this variation in the wheat crop, by procedures analogous to those used in the present work, will become routine.

SUMMARY

1. *Triticum aestivum* ssp. *vulgare* variety Chinese Spring ($2n = 6x = 42$) is susceptible to yellow rust caused by *Puccinia striiformis* while the wild annual grass *Aegilops comosa* ($2n = 14$) is resistant to all the physiologic races for which it has been tested.

2. By a backcrossing programme initiated from Chinese Spring × *Ae. comosa* hybrids, using Chinese Spring as the recurrent parent, a line was isolated with a single chromosome of *Ae. comosa*, determining rust resistance, added to the full complement of Chinese Spring.

3. The alien chromosome substituted with good genetic compensation only for the chromosomes of homoeologous group 2 of Chinese Spring. This demonstrated that the chromosome determining rust resistance is in homoeologous group 2. It was designated 2M since *Ae. comosa* has the M genome.

4. In order to induce recombination between 2M and its wheat homoeologues, hybrids were made using *Ae. speltoides* which has the capacity to suppress the activity of chromosome 5B that normally prevents homoeologous synapsis. A backcrossing programme, using Chinese Spring as the recurrent parent, was reinitiated from the 29-chromosome hybrids carrying chromosome 2M and the haploid complements of Chinese Spring and *Ae. speltoides*.

5. Selection was practised for rust resistance and ultimately a resistant plant with 42 chromosomes, that formed 21 bivalents at meiosis, was isolated. This plant was heterozygous for a dominant rust resistance allele (Yr_8) derived from *Ae. comosa*. Homozygotes were isolated in its progeny and in this way the rust resistant breeder's variety, Compair, was established.

6. Compair differs from Chinese Spring in its yellow rust resistance which was shown to be determined by a chromosome corresponding to 2D of Chinese Spring. This chromosome of Compair has the short arm, the centromere and a proximal segment of the long arm of chromosome 2M and a distal segment of the right arm of chromosome 2D. The modified chromosome, which is designated 2M/D, arose by homoeologous recombination in the *Ae. speltoides* hybrid or in the immediately succeeding backcross generations. Chromosome 2M/D carries the Yr_8 gene in the proximal segment of the long arm derived from chromosome 2M.

7. In hybrids between Compair and standard wheat varieties, chromosome 2M/D

pairs regularly with chromosome 2D so that regular segregation of Yr_8 can be expected and Compair treated like any other parental variety in wheat hybridization programmes.

8. This work illustrates the way that homoeologous recombination can be induced and exploited both in cytogenetic analysis in wheat and in practical breeding work. The nature of the meiotic synapsis of chromosome 2M/D with its partial homologues raises questions concerning the means by which chromosome 5B influences the specificity of meiotic synapsis.

REFERENCES

FELDMAN, M. (1966). The effect of chromosomes, 5B, 5D and 5A on chromosome pairing in *Triticum aestivum*. *Proc. natn. Acad. Sci., U.S.A.* **55**, 1447–1453.

JOHNSON, R. (1966). The substitution of a chromosome from *Agropyron elongatum* for chromosomes of hexaploid wheat. *Can. J. Genet. Cytol.* **8**, 279–292.

JOHNSON, R. & KIMBER, G. (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. (1966). Estimate of the number of genes involved in the genetic suppression of the cytological diploidization of wheat. *Nature, Lond.* **212**, 317.

MACER, R. C. F. (1966). The formal and monosomic genetic analysis of stripe rust (*Puccinia striiformis*) resistance. *Proc. 2nd Int. Wheat Genet. Symp.* (J. Mackey, ed.) *Hereditas* Suppl. **2**, 127–142.

MORRISON, J. W. (1953). Chromosome behaviour in wheat monosomics. *Heredity, Lond.* **7**, 203–217.

RILEY, R. (1960). The diploidisation of wheat. *Heredity, Lond.* **15**, 407–429.

RILEY, R. (1965). Cytogenetics and the evolution of wheat. In *Essays on Crop Plant Evolution* (J. B. Hutchinson, ed.), pp. 103–122. Cambridge University Press.

RILEY, R. (1966). The genetic regulation of meiotic behaviour in wheat and its relatives. *Proc. 2nd Int. Wheat Genet. Symp.* (J. Mackey, ed.). *Hereditas* Suppl. **2**, 395–406.

RILEY, R. & CHAPMAN, V. (1958). Genetic control of the cytologically diploid behaviour of hexaploid wheat. *Nature, Lond.* **182**, 713–715.

RILEY, R. & CHAPMAN, V. (1964). Cytological determination of the homoeology of chromosomes of *Triticum aestivum*. *Nature, Lond.* **203**, 156–158.

RILEY, R. & CHAPMAN, V. (1966). Estimate of the homoeology of wheat chromosomes by measurements of differential affinity at meiosis. In *Chromosome Manipulations and Plant Genetics* (R. Riley and K. R. Lewis eds.), a supplement to *Heredity, Lond.* **20**, 46–58. Edinburgh: Oliver and Boyd.

RILEY, R., CHAPMAN, V. & JOHNSON, R. (1968). Introduction of yellow rust resistance of *Aegilops comosa* into wheat by genetically induced homoeologous recombination. *Nature, Lond.* **217**, 383–384.

RILEY, R., CHAPMAN, V. & MACER, R. C. F. (1966). The homoeology of an *Aegilops* chromosome causing stripe rust resistance. *Can. J. Genet. Cytol.* **8**, 616–630.

RILEY, R. & KEMPANNA, C. (1963). The homoeologous nature of the non-homologous meiotic pairing in *Triticum aestivum* deficient for chromosome V (5B). *Heredity, Lond.* **18**, 287–306.

RILEY, R. & KIMBER, G. (1966). The transfer of alien genetic variation to wheat. *Rep. Pl. Breed. Inst.* 1964–65, 6–36.

RILEY, R. & LAW, C. N. (1965). Genetic variation in chromosome pairing. *Adv. Genet.* **13**, 57–114.

SEARS, E. R. (1953). Nullisomic analysis in common wheat. *Am. Nat.* **87**, 245–252.

SEARS, E. R. (1954). The aneuploids of common wheat. *Bull. Mo. agric. Exp. Sta.* 572.

SEARS, E. R. (1956). The transfer of leaf rust resistance from *Aegilops umbellulata* to wheat. *Brookhaven Symp. Biol.* **9**, 1–22.

SEARS, E. R. (1966). Nullisomic-tetrasomic combinations in hexaploid wheat. In *Chromosome Manipulations and Plant Genetics*. (R. Riley and K. R. Lewis, eds.), a supplement to *Heredity, Lond.* **20**, 29–45. Edinburgh: Oliver and Boyd.