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INTRODUCTION

It has long been known that the 21 pairs of chromosomes of hexaploid wheat fall into three groups of seven, with each group, or genome, presumably derived from a different diploid ancestor. Relatively recently it has been discovered (SEARS, 1954, 1966) that the 21 different chromosomes can also be grouped into seven sets of three. Within each of these seven "homoeologous" groups, the three chromosomes have largely the same genetic content, for the tetrasome of each compensates to a substantial extent for the nullisome of each of the other two.

Studies of RILEY and CHAPMAN (1958a), RILEY (1960) and RILEY and KEMPANNA (1963) clearly show that in the absence of chromosome 5B a substantial amount of non-homologous pairing occurs and that this involves only, or almost only, homoeologues. Thus, the homoeologues have homologous segments long enough to support pairing and crossing over.

Unfortunately the nullisomic-tetrasomic test of homoeology is not highly sensitive (SEARS, 1966), and a short segment in common between two non-homoeologous chromosomes could easily escape detection. Such a segment might well be too short ever to lead to pairing and thus would also fail to be discovered by cytological means. Nevertheless it is likely that the homoeologous groups account for the very large part of the homologies among the chromosomes of wheat.

At least some of the chromosomes of a number of species related to wheat fall into the homoeologous groups also. The evidence is thus far mainly genetic, being that particular alien chromosomes are able to substitute for particular wheat chromosomes.

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Relationships of Rye Chromosomes

There is reason to think that each of the seven chromosomes of rye can be allocated to a particular homoeologous group. It has long been known that the hairy-neck chromosome of rye (chromosome I of O'Mara, 1951, and Riley and Chapman, 1958b) can be successfully substituted for 5A of wheat (Kattermann, 1938; O'Mara, 1946) and Muramatsu (personal communication) showed that this chromosome also substitutes for 5D. Riley (1965) was able to substitute rye chromosome II for all three wheat chromosomes of group 6 but no others. Acosta (unpublished Ph.D. thesis, 1961) found that a chromosome (not I, II, or III) of rye substitutes for at least two chromosomes of group 3. In the present paper it will be shown that III of rye belongs to homoeologous group 2. It is probably not too optimistic to assume that the remaining three chromosomes of rye will fall into groups 1, 4, and 7, respectively.

The available genetic data suggest that the rye chromosomes are almost as closely related to their wheat homoeologues as the latter are to each other. The cytological data, however, show little or no tendency of rye chromosomes to pair with those of wheat, even when the inhibitory effect of chromosome 5B is removed. In the only really critical study, Riley and Kimber (1966) were unable to observe any pairing of a telocentric for 6R in hybrids having the 5B effect suppressed by the *T.* (*Ae.*) *speltoides* genome. They emphasized the "inconsistency between the genetic affinities of the chromosome and its pairing properties". Riley (1960) found only about the same frequency of quadrivalents in nulli-5B wheat-rye hybrids as in nulli-5B wheat haploids.

Relationships of Agropyron *Chromosomes*

Five *Agropyron* chromosomes of known origin have been studied, three from *A. elongatum* and two from *A. intermedium.* At least four of the five substitute very successfully for particular wheat chromosomes.

Knott (1964) found that an *A. elongatum* chromosome which conditioned stem-rust resistance in wheat tended to substitute spontaneously for chromosome 6A. The substitution lines were barely distinguishable from the recipient variety, even in such specialized characters as grain yield and flour quality. Also, pollen carrying the *Agropyron* chromosome instead of 6A competed on equal terms with normal pollen. Johnson (1966) and Anderson and Driscoll (1967) succeeded in substituting this same *Agropyron* chromosome for 6D, and Anderson and Driscoll found the substitution to be "vigorous and fully fertile".

The other two *A. elongatum* chromosomes, each conditioning resistance to leaf rust, substitute very well for 3D (Bakshi and Schlehuber, 1958) and 7D (Quinn and Driscoll, 1967; Knott, pers. comm.), respectively.

One chromosome of *A. intermedium* compensates so well for a particular wheat chromosome that the rust-resistant substitution line is grown commercially, under the name "Weique" (Wienhues, 1965, and pers. comm.). A second resistance-carrying *intermedium* chromosome has also been substituted for wheat chromosomes, and lines obtained that are reasonably vigorous and fertile (WIENHUES, 1966, and pers. comm.). The various wheat chromosomes concerned ostensibly belong to several different homoeologous groups, but the possibility of monosomic shift appears not to have been entirely ruled out. RILEY (1966) and JOHNSON (1966) emphasize the danger of such shift and the consequent involvement of different chromosomes than expected in substitution lines.

In estimating the closeness of relationship of the *Agropyron* chromosomes to those of wheat, one must bear in mind that the wheat chromosomes of each homoeologous group differ from each other, and to different degrees (SEARS, 1966). An alien chromosome which compensates fully for any one wheat chromosome can be expected to compensate well for a second member of the same homoeologous group only if that wheat chromosome is very closely related to the first wheat chromosome.

KNOTT's chromosome, which is very closely related to 6A, shows the expected close relationship to 6D, which is closely homoeologous to 6A. Homoeology is less with 6B, in accordance with the somewhat anomalous position of 6B in the group. If a prediction were to be made on the basis of this one chromosome, it would have to be that the *Agropyron* genome concerned is most closely related to the A genome of wheat.

Since 3D and 7D belong to homoeologous groups in which relationships are very close (SEARS, 1966), the *A. elongatum* homoeologues may be expected to substitute well for 3A and 3B, and 7A and 7B, respectively, and it would be premature to conclude that they come from a genome or genomes more closely related to D than to any other.

On the basis primarily of the results with group 6 chromosomes, but also in view of the information with respect to *Agropyron* substitutions for groups 3 and 7 and rye substitutions for groups 2, 3, and 5, it appears that *A. elongatum* chromosomes are genetically more closely related to wheat chromosomes than are those of rye. Although the *Agropyron* chromosomes concerned could be a non-random sample with respect to their closeness to wheat, there is no good reason for thinking so, for they were selected not for their ability to substitute successfully for wheat chromosomes but rather for their effect on reaction to disease organisms.

On the cytological side, what little evidence there is suggests that there is not much pairing of *Agropyron* with wheat chromosomes when the 5B effect is neutralized. JOHNSON and KIMBER (1967) found 4.8% pairing of a telocentric of KNOTT's chromosome in hybrids having the 5B effect suppressed. Wheat telocentrics paired in 51.1% of the same microsporocytes.

Relationships of Aegilops Chromosomes

In spite of the fact that at least one, and probably two, of the three genomes of wheat come from the Aegilops section of the genus *Triticum*, the data available on relationships of Aegilops chromosomes (other than those of the

D and supposed B genomes) with wheat chromosomes are mainly cytological. Only two substitutions have been reported. Riley, Chapman and Johnson (1968) isolated a chromosome from *T. comosum* (*Ae. comosa*) which substitutes for wheat chromosomes of group 2. That pairing of this chromosome occurs when the 5B effect is suppressed is attested to by the fact that an exchanged chromosome, partly 2M and partly 2D, was obtained. Another substitution obtained by Riley (personal communication) involves a chromosome of *T. bicorne* (*Ae. bicornis*) and an unidentified wheat chromosome.

Riley, Chapman and Kimber (1959) and Riley and Law (1965) have provided ample cytological evidence that the chromosomes of *T. longissimum* (*Ae. longissima*), *T. comosum, T. dichasians* (*Ae. caudata*), and *T. umbellulatum* (*Ae. umbellulata*) pair to a substantial extent with wheat chromosomes—presumably homoeologues—in the absence of chromosome 5B.

Although it is now generally assumed that *T. speltoides* is the source of the B genome, there is still no cytological confirmation of this. In fact, Riley and Chapman (1966), on the basis of careful study of the pairing affinities of the chromosomes of group 5, suggested that the hybrid *T. speltoides* with *T. aestivum* "would show little or no meiotic pairing were the 5B activity not suppressed". Kimber's (1966) results with *speltoides*-like derivatives from *speltoides* x *T. longissimum* (*Ae. sharonensis*) backcrossed two times to *speltoides* with selection for *longissimum* 5B activity tend to confirm the conclusion of Riley and Chapman. When Kimber crossed the backcross derivatives with *T. aestivum*, an average of only 2.9 bivalents were formed by the hybrids, which is but 1.7 bivalents more than Riley (1960) found in haploids of *T. aestivum*. Thus, although the BC_2 plants should have had about 7/8 of their chromosomes from *T. speltoides*, fewer than two of these chromosomes paired, on the average, and they almost never formed ring bivalents. As Riley and Chapman (1966) pointed out, if *T. speltoides* is indeed the source of the B genome, its chromosomes must have undergone marked changes since their incorporation in polyploid wheat. Perhaps, as Sarkar and Stebbins (1956) suggested, the B genome is a composite of chromosomes or chromosome segments from several species of the *speltoides* complex.

The pattern which thus seems to be emerging is one of remarkably close relationship between chromosomes of common ancestry, not only from the A, B, and D genomes of wheat, but also from rye and at least some of the species of *Agropyron* and Aegilops. Although the nullisomic-tetrasomic and alien-substitution tests are not sensitive enough to rule out minor homologies with other chromosomes than those in the same homoeologous group, it appears that nearly all the homology can be accounted for within groups.

Chromosome III of Rye

The evidence that chromosome III of rye belongs to homoeologous group 2 comes from two sources: (1) It has substantially the same effect when added to Chinese Spring wheat as has extra dosage of group 2 chromosomes; namely, it increases awn length and makes leaves narrower, culms more slender, and glumes smaller and stiffer (Fig. 1b). (2) A pair of telocentric rye chromosomes in the very vigorous Cornell wheat selection 82a1-2-4-7 is substituted for one arm of chromosome 2B, and the rye telocentric concerned is an arm of rye III. In view of this and the additional evidence to be presented, rye chromosome III will henceforth be designated 2R.

EXPERIMENTAL

The 2R chromosome used in this study was derived from an inbred of the variety Imperial produced by Dr. H. L. SHANDS at the University of Wisconsin. The wheat was Chinese Spring.

In the production of substitution lines involving 2R, the addition line was first crossed to monosomics 2A, 2B, and 2D. Cytological study of offspring with $20'' + 2'$ revealed no pairing of the rye and wheat monosomes. These offspring were pollinated onto the addition line. It was assumed that if 2R is homoeologous to the group 2 chromosomes, pollen with 2R substituted would sometimes function, and offspring would be produced with 20 wheat disomes, a rye disome, and a wheat monosome.

The Substitution for 2B

In the experiment with chromosome 2B (XIII), three plants with $21'' + 1'$ were obtained from the cross of $21'' + 1''2\text{R} \times 20'' + 2'2\text{B},2\text{R}$. Of the two of these tested, one proved to have a 2R disome, of which, however, one member was an isochromosome. Among the progeny of this plant from selfing, those lacking 2B were easily identifiable by their lack of bloom, since chromosome 2B carries a gene for the production of bloom (MURAMATSU, pers. comm.). None of the four bloomless plants obtained had $21''$. Two had $20'' + \text{i}1''$, one had a telocentric monosome, and one a complete monosome.

Among 17 offspring of the substitution monosomic, none of the 12 plants that could be classified was disomic. Five were nullisomic, six monosomic, and one had iso plus complete. The high frequency of nullisomics showed that 2R does not compensate fully for 2B in the pollen.

Of 17 offspring from $20'' + \text{i}1''$, only one had a pair of normal 2R's. This substitution plant (Fig. 1c), besides being bloomless, was characterized by toughness of glumes and partial sterility. That it was even partially fertile is evidence of homoeology of 2R and 2B, for nulli-2B is fully female-sterile.

The Substitution for 2D

Substitution of chromosome 2R for 2D was not easily made, although 2R is enough longer than 2D that a 2R univalent can always be distinguished from a 2D univalent when both are present in the same cell. With only one univalent present, however, identification may be less than certain. From $21'' + 1''2\text{R} \times 20'' + 2'2\text{D},2\text{R}$, two of 15 offspring were thought to have $20'' + \text{t}1''2\text{R} + 1'2\text{D}$, but tests showed that both were $\text{t}1''2\text{D} + 1'2\text{R}$.

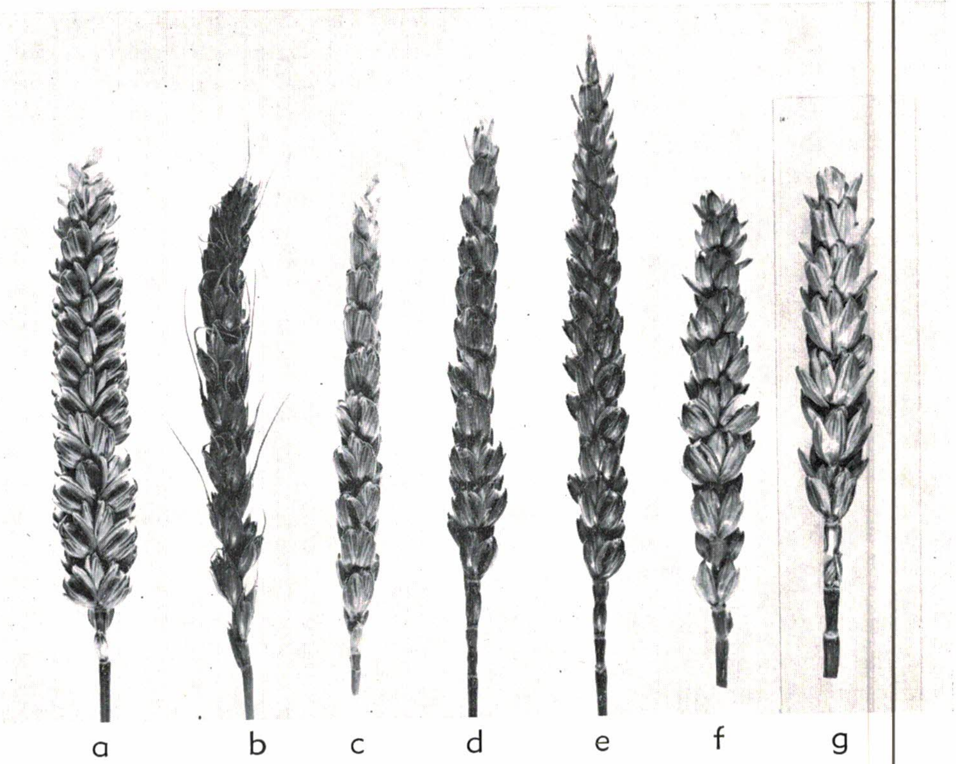

FIG. 1. Spikes of (a) normal Chinese Spring wheat, (b) disomic addition of 2R, (c) disomic substitution of 2R for 2B, (d) disomic substitution of 2R for 2D, (e) substitution of telo 2R + complete 2R for 2D, (f) disomic substitution of 2R telocentric for 2D, and (g) nullisomic 2D.

From a plant with 20″ + 2′2D,2R selfed, one of ten plants was correctly classified as 20″ + 1′2R. Selfing of this substitution monosomic gave rise to no offspring with 20″ + 1″2R. Instead, three plants were nullisomic, three were monosomic, three had 20″ + t′, one had 20″ + i′, one had 20″ + i1″, and one had 20″ + t1″. The data suggested little transmission of the entire chromosome through the pollen, but reasonably good male transmission of telocentrics and isochromosomes derived from it. Although misdivision of the 2R monosome appeared to be about twice as frequent as had previously been observed for 5A (SEARS, 1952), this did not seem to be the sole cause of the very low male transmission of the complete 2R.

That the telocentric derivative substitutes better for 2D in pollen than the complete 2R does, is clear from the results of selfing the plant with 20″ + t1″2R. Eight plants were of the parental phenotype, seven had 20″ + t″, and one had 20″ + t′. These results are compatible with the conclusion that only the telo was transmitted through the pollen, whereas half the eggs carried a complete 2R and half the telocentric. A subsequently grown, larger progeny of 25 from

20″ + t1″2R included two with a pair of complete 2R chromosomes, showing that pollen with the complete chromosome does not fail entirely.

Plants carrying either a pair of complete 2R chromosomes (Fig. 1d) or one complete and one telocentric (Fig. 1e) were superior in size and fertility to those with only a pair of telocentrics (Fig. 1f). Whereas four plants with a telocentric pair averaged only 3.5 seeds (range 0 to 7), the single plant observed with a complete pair had 31 seeds, and seven plants with one telo and one complete averaged 25.4 (6 to 49). The arm missing in the telocentric carries a promoter or promoters of awn development and glume stiffness, and therefore the ditelosomic plants are fully awnless, like nulli- 2D (Fig. 1g), and soft-glumed. The gene (or genes) for glume stiffness is more effective than that of 2D (or 2B), giving the substitution line stiffer glumes than Chinese Spring. The effect on the spike of substituting 2R for 2D (or 2B) may be summarized as a tendency toward speltoidy.

The Attempted Substitution for 2A

When a plant which was mono-2A (II), mono-2R was crossed as male to the 2R disomic addition, it was expected to yield one or more plants of the constitution 20″ + 1″2R + 1′2A. These would presumably be distinguishable from 21″ + 1′2R by the shortness of chromosome 2A relative to 2R. In fact two plants believed to be 20″ + 1″2R + 1′2A were obtained (in a progeny of 12). Neither had a complete rye disome: in one the 2R disome included a telocentric and in the other an isochromosome. The latter plant was chosen as a possible source of offspring with a complete rye disome.

From the plant with 20″ + i1″2R + 1′2A, five offspring were analyzed cytologically (from a population of 20). One of these had 21″ and was atypical for Chinese Spring wheat. Pollinated by 20″ + t″$_{s}$2A, its only analyzed offspring had 20″ + 1′ + t′, indicating that the 21″ plant had a 2R pair substituted for 2A.

A selfed progeny from the 21″ plant was grown, and a 21″ daughter was pollinated onto mono-2A. From this cross, those offspring with the full chromosome complement had a heteromorphic bivalent which paired in one arm only. Chromosome 2A was clearly involved, for the heteromorphic bivalent was lacking in the plants deficient for 2A. The free arm of the second chromosome was substantially longer than that of 2A. Pairing of these two chromosomes occurred in every one of the 50 microsporocytes examined.

Since the heteromorphic bivalent was never involved in pairing with another wheat chromosome, the arm which failed to pair with 2A cannot have come from a wheat chromosome, but must have come from 2R. Presumably the exchange occurred in the plant which had i1″2R + 1′2A. When the isochromosome paired on itself rather than pairing with the complete 2R, as it frequently did, the complete 2R was free to pair homoeologously with 2A. Although such pairing would be expected to occur rarely, if at all, in the presence of chromosome 5B, a single occurrence cannot be ruled out. Alternatively, the two univalents may have misdivided and a reunion occurred of a 2R arm with a

2A arm, as suggested by MORRISON (1954). In this case, the interchanged chromosome would have its break point in the centromere. The exchange chromosome apparently includes $2A_L$ rather than $2A_S$.

Plants presumably disomic for the interchanged chromosome are conspicuously more nearly normal in morphology and fertility than are 2R(2B) or 2R(2D) substitution plants.

DISCUSSION

Chromosome 2R substitutes reasonably well for chromosomes 2B and 2D of wheat. The 2R(2A) substitution is not yet available. Since 2A is the anomalous one of the three wheat homoeologues, the degree of compensation of 2R for 2A is unlikely to be closely similar to that for 2B and 2D. It may be either worse or better.

Judging from the amount of compensation shown by rye chromosomes 5R and 6R for their wheat homoeologues, 2R appears to be about average in its degree of relationship to its homoeologues.

In order to determine the amount of pairing that is possible between 2R and its wheat homoeologues, each group 2 chromosome is being combined as a monosome with a 2R monosome in a nulli-5B plant. The method being used is the following:

Monosomic 2A (or 2B or 2D) is pollinated by mono-iso-5B. From this cross, occasional plants with $19'' + 2'$2A,5B, occur, as a result of the functioning of nulli-5B pollen (8 obtained among 82 offspring). If no such plant is found, one with $19'' + i1''$5B $+ 1'$2A can be selected and a $19'' + 2'$ individual isolated in the next generation (3 obtained among 61 offspring).

From a cross of $19'' + 2'$2A,5B by the appropriate disomic substitution line, $20'' + 1''$2R(2A), about 9/16 of the offspring should be $19'' + 2'$2R,5B. A plant of this constitution can then be pollinated by the disomic line, and about 3/16 of its offspring will have the constitution $19'' + 1''$2R $+ 1'$5B. Pollination of one of these by nulli-5B, tetrasomic-5D (or some other line deficient for the 5B inhibitor of homoeologous pairing) will yield offspring of which about 3/4 will have $18'' + 1'''$5D $+ 2'$2A,2R. Since these plants will be nulli-5B, the 2A and 2R monosomes will have every opportunity to pair.

From the results of RILEY and KIMBER (1966), little or no pairing of 2A (or 2B or 2D) with 2R can be expected. If they do pair, the recombined chromosomes can be recovered simply by crossing with normal. The offspring will be mono-5B, and hence will have no homoeologous pairing. Recombined 2A-2R chromosomes will be identifiable by their ability to pair with 2A although each carries one or more genes from rye.

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