M. Feldman

GENETIC SUPPRESSION OF HOMOEOLOGOUS PAIRING IN WHEAT BREEDING *

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The 21 pairs of chromosomes of hexaploid wheat, *Triticum aestivum* L., belong to three different but related genomes, A, B, and D. Eeach of the seven chromosomes of each genome has a homoeologue (chromosome homologous in part) in each of the other two genomes. Pairing of homoeologues is prevented by a dominant gene on chromosome 5B (Okamoto, 1957; Riley, 1958; Sears and Okamoto, 1958). This gene, according to Feldman (1966), operates by reducing the intensity of somatic association, thereby assuring that homologues enter meiosis lying closer to each other than to their homoeologues.

Many of the relatives of wheat have chromosomes which are homoelogous to those of wheat. It has long been known that the hairy-neck chromosome of *Secale cereale* can successfully be substituted for the speltoid chromosome (5A) of wheat (Kattermann, 1937), thus indicating homoeology; and several additional chromosomes of rye have recently been found capable of substituting for other wheat chromosomes (Jenkins, 1966; Riley, 1965; Sears, unpublished). At least three different chromosomes of *Agropyron* have been found to substitute very well for certain wheat chromosomes (Caldwell, et al., 1956; Knott, 1959; Bakshi and Schlehuber, 1959; Wienhues, 1962; Sharma and Knott, 1966), and there is every reason to think that the chromosomes of most or all diploid *Aegilops* species will prove to have wheat homoeologues. Although no substitutions for wheat chromosomes have yet been reported of chromosomes of *Haynaldia,* the remaining genus of the sub-tribe *Triticinae,* it is reasonable to asume that at least some of these chromosomes too will fall into the homoeologous groups.

Chromosomes from the genera related to wheat normally pair little or not at all with their wheat homoeologues, but presumably many of them can be induced to pair by elimination or suppression of the effect of chromosome 5B. This should make possible the transfer of foreign genes to homoeologous wheat chromosomes through crossing over.

Genes for disease and insect resistance and other genes desired by breeders occur in many of the related species. Riley and Kimber (1966) point out that it is not unreasonable to expect that genes for improvement of yield will also be obtainable from these relatives.

Genes transferred through induced homoeologous pairing should usually be less deleterious than those transferred with the aid of radiation, as by Sears (1956), Knott (1961), Sharma and Knott (1966), Wienhues (1962), Acosta (unpublished Ph. D. thesis), and Driscoll and Jensen (1963). Radiation-induced transfer normally involves the substitution of a segment of a foreign chromosome for a wheat segment. Since the piece of wheat chromosome replaced is unselected, the foreign segment is very unlikely to compensate for it fully. On the other hand, a segment transferred to a homoeologous chromosome through pairing and crossing over may well correspond quite closely to the segment replaced and thus have no deleterious effect.

There are several ways in which suppression of the 5B effect may conceivably be utilized in the transfer of genes to wheat. The simplest is to cross a monosomic-5B plant with a foreign species and select offspring lacking chromosome 5B. These will have homoeologous pairing. However, the increased pairing

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will tend to reduce or suppress the formation of restitution nuclei, and this may in turn cause the hybrids to be nearly or completely sterile. Their offspring, if any, will be highly aneuploid, making difficult the recovery of a particular wheat chromosome to which a desired gene has been transferred. Riley and Kimber (1966), however, report the transfer in this way of characters of *T. bicorne* (=*Ae. bicornis*) to *T. aestivum*.

Doubling the chromosome number of the 5B-deficient hybrid renders it reasonably fertile, but then each chromosome has a homologue, and relatively little homoeologous pairing can be expected to occur.

There are certain advantages to working with a single foreign chromosome at a time. This may be done by adding the desired foreign chromosome to a plant which is monosomic for one of the chromosome's wheat homoeologues. Such plants are easily obtained by crossing normal wheat to an alien-substitution line (figure 1). If the double-monosomic hybrids are at the same time nullisomic 5B, the two homoeologues should pair at maximum frequency, for neither has a homologue to compete for pairing. Nulli-5B plants, however, are so low in vigor and fertility that recovery of interchanged chromosomes may be difficult.

Recovery and identification of the desired interchanged chromosomes obtained by this and other methods of using induced homoeologous pairing may be made by backcrossing to normal (figure 1). Where the desired segment of the foreign chromosome has been transferred to the homoeologous wheat monosome, the plant concerned will have the phenotype conditioned by the foreign segment, but the chromosome concerned will pair with a wheat chromosome. There will not be homoeologous pairing, since the one dose of normal 5B supplied by the normal parent will be sufficient to suppress such pairing.

The problem of infertility of nulli-5B can be largely overcome by incorporation of tetrasome 5D. This means, however, that the plants in which homoeologous exchange is expected will have a nullisome two monosomes, and a tetrasome or trisome. Obtaining and identifying these complex aneuploids may be simplified by use of a substitution line which has been made monosomic for chromosome 5B in preparation for the cross to nulli-5B tetra-5D (figure 2). By using the latter as male, offspring are obtained of which approximately 75% are of the desired constitution and easily recognizable as such. Since chromosome 5D apparently has an effect on homoeologous pairing opposite to that of 5B (Feldman, 1966), there is a possibility that the extra dose of 5D in the nulli-5B plants will lead to an increase in pairing of the homoeologues over what would be induced by simple nullisomy for 5B. At any rate, this method deserves a serious trial.

An alternative way of obtaining pairing of the foreign monosome with the homoeologous wheat monosome is to introduce the genome of *T. speltoides* (= *Ae. speltoides*), which inhibits 5B action (Riley, Kimber, and Chapman, 1961). This can be done by using an amphiploid *T. aestivum* × *T. speltoides* to cross with the alien-substitution line. However, the *speltoides* chromosome set supplies an additional homoeologue to compete for pairing with the foreign chromosome and its wheat homoeologue.

For most efficient use of the 5B effect, it will perhaps be necessary to have a deficiency or null mutation of the gene concerned. When a line carrying such a mutation is crossed with a mono-5B alien-substitution line (figure 3), hybrids will be obtained which are hemizygous for the pairing mutation and monosomic for both the foreign chromosome and its wheat homoeologue. Such plants will have homoeologous pairing and should be highly fertile.

Mutation rates of over 3% have been obtained in preliminary radiation experiments with the 5B suppressor of homoeologous pairing (Okamoto, 1962; Sears, unpublished). However, a useful mutation should be freely transmissible through the pollen and should not be deleterious when homozygous. Most or all radiation-induced mutations will be deficiencies, with degrees of deleteriousness dependent upon the lengths of the deficiencies concerned. Since it is unknown whether the pairing gene is proximal or distal in the arm, there is no way to predict what fraction of the mutations obtained may be short enough not to be deleterious. The fraction will be small if the location of the gene is proximal, because terminal deletions including the locus will necessarily involve nearly the entire arm. Terminal deletions are a very common type of deficiency obtained following irradiation of wheat (Steinitz-Sears and Sears, 1957).

At present the only reliable way of detecting mutations of the pairing gene is to test each irradiated chromosome in a wide hybrid for its ability to cause homoeologous pairing. Because of the ease with which some varieties of rye cross with wheat, this appears to be the best species to use for making the hybrids. Unfortunately rye can only be used as the male parent, which greatly increases the labor involved in testing mutations for male transmission from heterozygotes. A mono-5B substitution line whose foreign chromosome pairs readily with its wheat homoeologue in the absence of chromosome 5B would presumably be excellent for testing male gametes.

An experiment is presently under way which involves the x-raying of normal pollen and the use of this on plants which have a genetically marked monosome 5B. Some 400 seeds have been obtained. Elimination of offspring with the marker will get rid of the disomics, totaling about 25%. There will presumably be a few plants among the remainder which have no paternal 5B; these will be discarded as nullisomics. Since deficiencies in chromosome 5B will be hemizygous, those which are strongly deleterious will be detectable and can be discarded. The remaining X_1 plants will be crossed with rye and the 28-chromosome offspring (that is, those which carry the 5B chromosome) will be examined for homoeologous pairing.

Mutations obtained will be maintained hemizygous by regular backcrossing to mono-isosomic $5B^L$. Hemizygosity is preferable to heterozygosity because nearly all male gametes of the hemizygote (monosomic 5B) will carry the mutation, and verification of the presence of the mutation will involve a mere cytological check for the presence of the 5B chromosome, not the slow and laborious crossing with rye and examining the hybrid offspring cytologically. At the same time, the continuous backcrossing will permit screening out translocations which may arise as a result of homoeologous pairing.

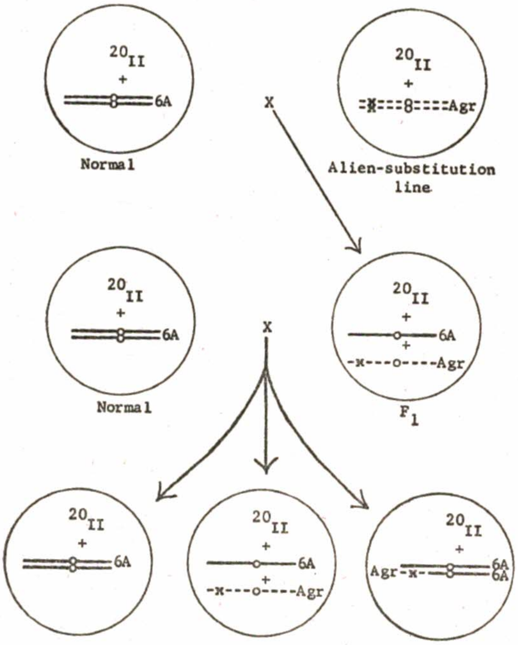

Figure 1. Use of a substitution line to obtain plants monosomic for a foreign chromosome (Agr) and its wheat homoeologue (6A), and suggested method for recovering interchanged chromosomes with the marker gene *x*.

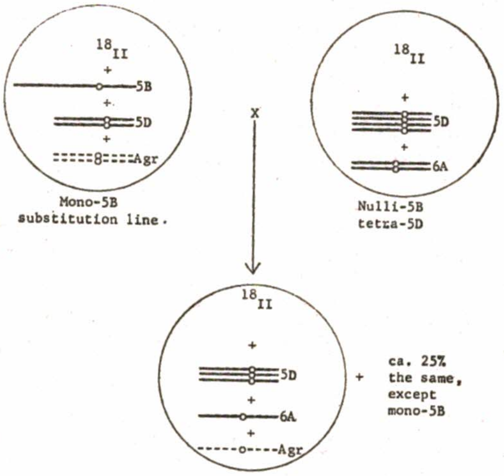

Figure 2. Suggested method for use of nullisomic-5B tetrasomic-5D to induce pairing of a foreign chromosome (Agr) and its wheat homoeologue (6A).

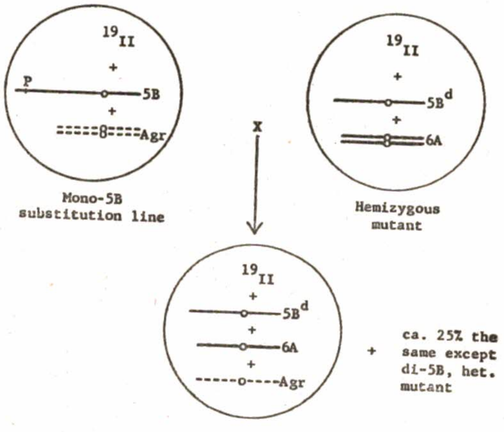

Figure 3. Suggested method for use of chromosome-5B deficiency to induce pairing of a foreign chromosome (Agr) and its wheat homoeologue (6A). *P* is the suppressor of homoeologous pairing.

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