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5 TRANSFER OF ALIEN GENETIC MATERIAL TO WHEAT

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As pointed out by Frankel (1970) and others, the pool of potentially useful genes available to wheat breeders has shrunk alarmingly in recent years, primarily because of the replacement of the highly variable land races in many parts of the world by higher-yielding, pure-line varieties. It appears that much of the genetic variability of the cultivated wheats has already been lost and cannot be recovered.

The picture becomes much brighter, however, when we realize that the relatives of wheat are accessible sources of genes for use in wheat improvement. The cultivated wheats are blessed with a large assortment of relatives (Table 5.1), diverse in phenotype and adaptation. They bring forth the pleasant prospect that wheats may be produced which are adapted to colder, hotter, drier, saltier, or less fertile environments; which have new genes for resistance; or which even have greater yielding capacity than existing cultivars when grown in present wheat-producing regions. Obviously, the more distant from wheat the relative is, the more likely it is to have genes that are not present in any of the wheats themselves. Some of these genes may be of great value to wheat growers.

Nearly all of the closer relatives can be crossed with wheat, especially if advantage is taken of such procedures as searching for crossable biotypes, stimulating seed development with growth hormones, and culturing embryos on artificial media. Even barley, which belongs to a different sub-tribe than wheat, has now been crossed with wheat (Kruse, 1973; Islam *et al.*, 1975; Fedak, 1977). Should any blocks to crossing be found, the desired hybrids can presumably be obtained by using the techniques of somatic-cell fusion, once these have been perfected.

Until the past 20 years, an almost insurmountable block to transfer of genes to wheat was the inability of wheat chromosomes to pair with those of any of its relatives except those few that have one or more genomes (sets of seven pairs of chromosomes) homologous with wheat genomes. Crosses were able to be made and hybrids grown, but failure of chromosome pairing all but precluded the transfer of alien genetic material to wheat chromosomes. To be sure, it was known that exchanges could be induced with ionizing radiation, and several genes for disease resistance were transferred to wheat in this way (reviewed by

Table 5.1

Groups of wild relatives of wheat, listed in decreasing order of their presumed closeness of relationship to common wheat (ABD)

Type of gene pool	Species and genomic formulae
1. Species with homologues of wheat genomes	
(a) The tetraploid progenitor	*T. turgidum* var. *dicoccoides* (AB)
(b) The diploid donors of the A and the D genomes	*T. monococcum* var. *boeoticum* or var. *urartu* (A) *T. tauschii* (D)
(c) Polyploids with one homologous genome	
(i) The A genome	*T. timopheevii* var. *araraticum* (AG)
(ii) The D genome	*T. crassum* (DM^{cr},DD_2M^{cr}) *T. ventricosum* (DM^{v}) *T. cylindricum* (CD) *T. juvenale* ($DM^{cr}U$) *T. syriacum* ($DM^{cr}S$)
2. Species with homoeologous genomes	
(a) Closely related species	
	T. searsii (S^{s}) *T. longissimum* (S^{l}) *T. sharonensis* (S^{l}) *T. bicorne* (S^{b}) *T. speltoides* (S) *T. variabile* (US^{v}) *T. kotschyi* (US^{v})
(b) Less closely related species	*T. tripsacoides* (Mt) *T. dichasians* (C) *T. comosum* (M) *T. umbellulatum* (U) *T. uniaristatum* (M^{u}) Other U-containing polyploids Several *Agropyron* species
(c) Distantly related species	Species of *Secale*, *Haynaldia*; numerous species of *Agropyron* and of other genera of the *Triticinae* and *Hordeinae*

Knott, 1971); but this is at best a very laborious process, with a low probability of yielding an acceptable transfer.

The failure of wheat chromosomes to pair with those of related species severely restricted the exploitation of the relatives. The chromosome number of a hybrid of wheat with a relative could be doubled, resulting in a fertile amphiploid, but these, with one exception, have never been commercially successful. The exception, *Triticale*, has up to seven rye pairs added to the 14 chromosome pairs of tetraploid wheat; but the rye chromosomes are not from a typical relative, which would be a wild species, but are from a cultivated species.

It is also possible to add almost any pair of alien chromosomes to wheat, producing an alien-addition line. This rarely, if ever, leaves the genotype well balanced. Also, loss of the alien chromosome is favoured by pollen selection, with the result that the line tends to return to the euploid condition.

A better stratagem for introducing alien variation is to substitute the alien chromosome pair for a homoeologous (related) pair of wheat chromosomes. This is easily accomplished by crossing the addition line onto the proper wheat monosomic and recovering an F_2 plant deficient for the wheat pair and disomic for the alien pair. This plant and the descendent alien-substitution line may be essentially normal in phenotype and of stable constitution, like several East European wheat cultivars that have chromosome 1R of rye substituted for wheat chromosome 1B (Mettin *et al.*, 1973; Zeller, 1973). Nearly always, however, the complete alien chromosome carries with it one or more undesirable genes, or else it does not compensate satisfactorily for the missing wheat chromosome.

A further possibility has been identified in recent years (Sears, 1972a): to substitute one arm of an alien chromosome for a corresponding wheat arm. This can be achieved by taking advantage of the fact that univalents in wheat frequently misdivide at meiosis I. If both the alien chromosome and its wheat homoeologue are monosomic, both will be univalent at meiosis. When both happen to misdivide in the same sporocyte and give rise to telocentric chromosomes, these will occasionally fuse at the centromeres to produce a bibrachial chromosome with one arm from the alien chromosome and one from the homoeologue. The frequency with which the correct combination arises is so low, however, that the amount of effort required is little, if any, less than would be needed to induce homoeologous pairing and replace only part of the wheat arm with the corresponding alien segment. Therefore whole-arm substitution is not likely to become a popular method for introducing alien variation.

Of great potential value to wheat breeding was the discovery by Okamoto (1957) and Riley and Chapman (1958; also Riley *et al.*, 1958) that the failure of related chromosomes to pair is due to a particular wheat chromosome, 5B. In the absence of 5B, not only homologues but also homoeologues can pair; but if

both modes are possible, homologous pairing is favoured over homoeologous. High levels of homoeologous pairing usually occur in hybrids that lack 5B (Figure 5.1).

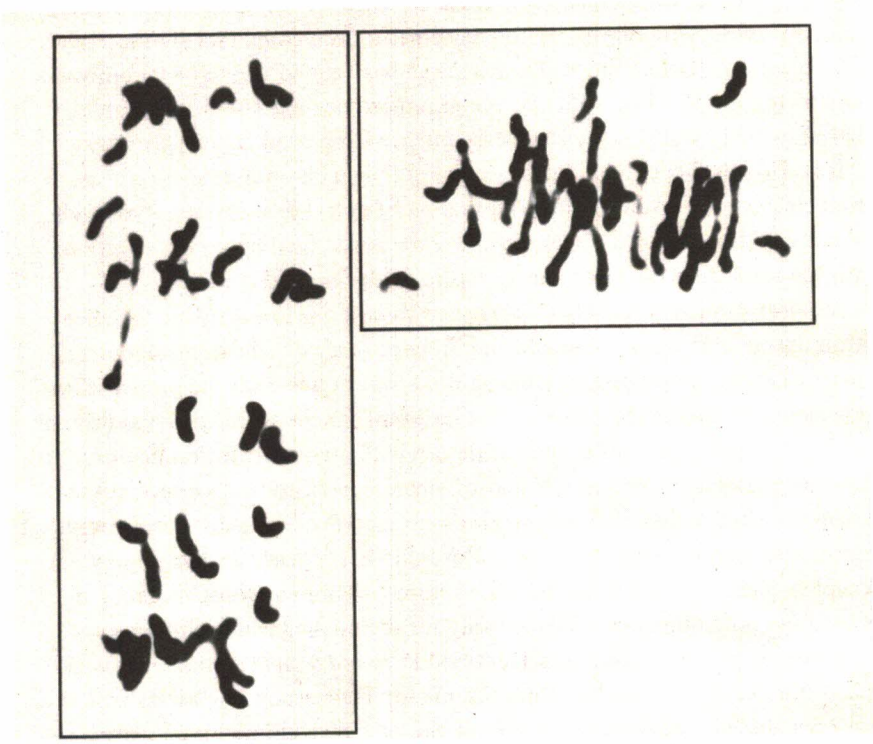

Fig. 5.1. Effect of the suppressor of homoeologous pairing, *Ph1*, on meiosis in the hybrid, hexaploid wheat (AABBDD) x *Triticum kotschyi* ($UUS^{V}S^{V}$). With *Ph1* present (left), 33 chromosomes are unpaired and only 2 paired, whereas with *Ph1* absent (right), only 6 chromosomes are unpaired and 29 paired.

To induce alien chromosomes to pair with their wheat homoeologues, it is only necessary to delete chromosome 5B. The simplest way to do this is to pollinate monosomic 5B by the desired alien species. About 75% of the offspring will be deficient for chromosome 5B. Riley (1966b) used this method to transfer genetic material from *Triticum bicorne* (*Aegilops bicornis*) to wheat, and Joshi and Singh (1979) succeeded in introducing rye genes into wheat in the same way. Instead of mono-5B, nullisomic-5B tetrasomic-5D could have been used, or, better, a mutant line *ph1b ph1b* (Sears, 1977) evidently deficient for the pairing suppressor *Ph1* (for pairing homoeologous).

A problem encountered with 5B- and *Ph1*-deficient hybrids is their extremely low fertility. The probability of recovering a desirable transfer of a particular alien gene to wheat is very low if only a few seeds are obtained on the F_1, for most transfers involve a relatively long alien segment, likely to carry deleterious genes as well as the one desired. The almost complete sterility of the F_1 may be attributed to the high level of pairing, which presumably reduces the frequency of failure of the first meiotic division and thereby cuts down on the formation of restitution nuclei.

The fertility should be better if a less effective pairing mutant were used – either the partial mutant *ph1a* obtained by Wall *et al.* (1971) or Sears' (1977) *ph2* mutant on 3DS. However, the increased fertility would be offset by a lower frequency of recombination between homoeologues; thus there might be no net gain unless the alien genome happened to be especially closely related to one of the wheat genomes. In that case, as Feldman and Sears (1981) have suggested, the intermediate-pairing mutant might permit good pairing between the closely related genomes while largely suppressing pairing of the other homoeologues.

Rather than deleting *Ph1*, it is possible to suppress its inhibitory activity by adding the chromosomes of certain strains of *T. speltoides* (*Ae. speltoides*) or *T. tripsacoides* (*Ae. mutica*). In simple hybrids of wheat with these strains, homoeologous pairing occurs (Riley *et al.* 1958; Riley, 1966a) and can result in the transfer of *speltoides* or *tripsacoides* segments to wheat chromosomes. Further, when a high-pairing wheat-*speltoides* (or -*tripsacoides*) amphiploid is crossed with another alien species, homoeologous pairing occurs in the F_1. However, the *speltoides* chromosomes can pair and recombine with the wheat chromosomes, and also with those of the other alien species, thereby adding to the difficulty of sorting out the desired transfers. Nevertheless, Riley *et al.* (1968) succeeded in recovering in this way a part-wheat, part-*T. comosum* chromosome that provides resistance to the stripe-rust fungus.

For the transfer of a particular gene from an alien species to wheat, a degree of simplification, and at the same time greater precision, can be achieved by first isolating the critical alien chromosome by producing an addition line. This will be a line with the complete complement of wheat chromosomes plus one alien pair. Such lines are relatively easy to obtain (Figure 5.2) and in fact already exist for most or all of the chromosomes of a number of relatives, including rye, several diploid *Triticum* species, *Haynaldia villosa*, *Agropyron elongatum*, and even barley. The alien-addition line can be converted to homoeologous pairing by introducing the *ph1b* mutation, or by making the line nullisomic-5B and tetrasomic, or trisomic, 5D (Sears, 1972a). If the alien chromosome is monosomic instead of disomic, it will pair more freely with its homoeologues; and if one of the wheat homoeologues is also monosomic, a still higher level of homo-

eologous pairing can be achieved. This has an advantage that may be substantial; namely, most or all of the resulting transfers will involve a particular wheat chromosome instead of being distributed among all three homoeologues (Sears, 1972a).

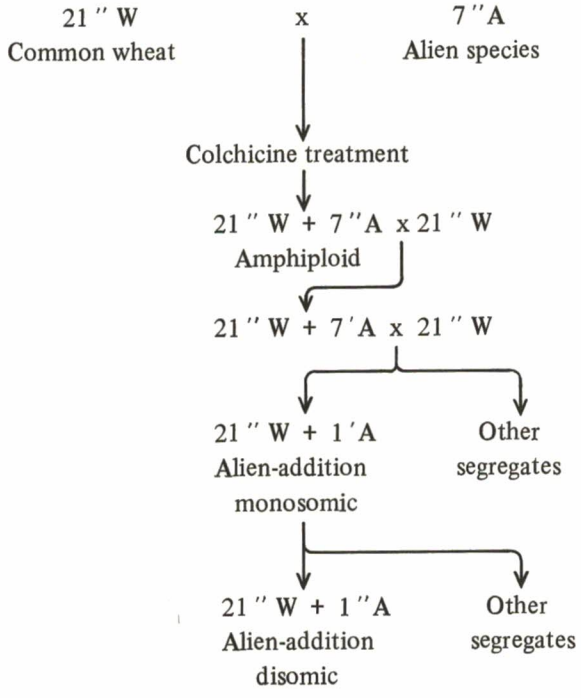

Fig. 5.2. Production of an alien-addition line. Alien species with 14 "may also be used. The colchicine treatment may be omitted, since the non-doubled hybrid pollinated by normal plants will usually give rise to a reasonable frequency of offspring with 21 "W + 7 'A, as the result of restitution-nucleus formation.

In order to make both an alien chromosome and its homoeologue monosomic, it is only necessary to obtain an alien substitution line (Figure 5.3) and cross it with a euploid. If the euploid is *ph1b ph1b* (or nulli-5B, tetra-5D) and the substitution line has been made monosomic-5B (Figure 5.4), the F_1 will be monosomic for both desired chromosomes and at the same time have homoeologous pairing (Figure 5.5).

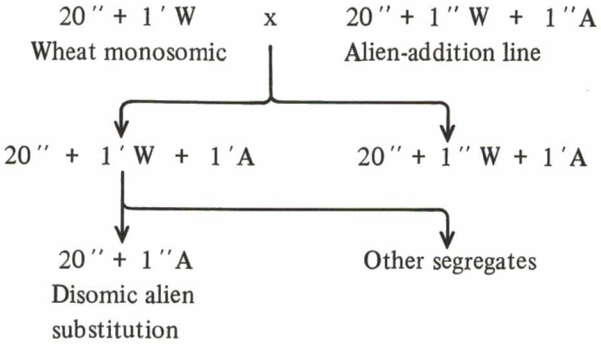

Fig. 5.3. Production of an alien-substitution line. From the plant with 20″+ 1′W + 1′A, a fair percentage of the functioning male gametes are expected to carry the alien chromosome instead of its wheat homoeologue.

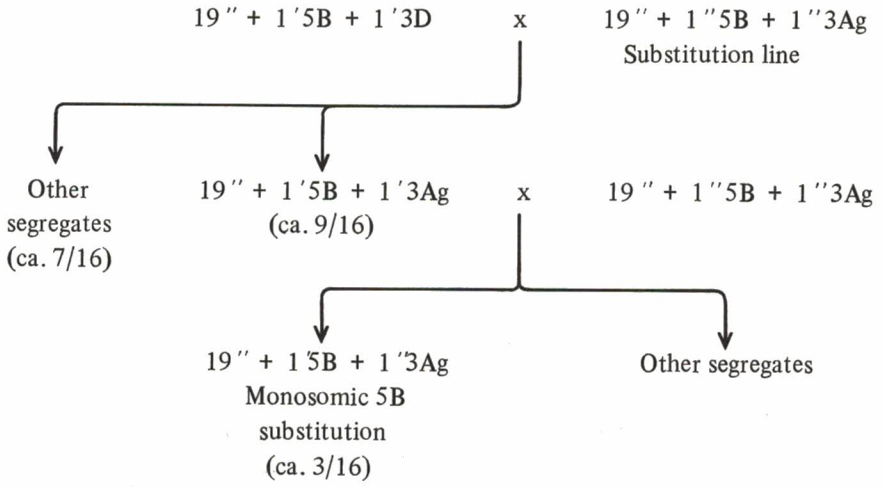

Fig. 5.4. One procedure for making a substitution line monosomic for chromosome 5B, as illustrated by the 3Ag(3D) substitution line.

Another step that may profitably be inserted into the procedure is to obtain a telocentric derivative (telosome) for the alien arm carrying the gene concerned and use this instead of the complete alien chromosome. The complete chromosome will have been monosomic at a previous stage and, since alien univalents tend to misdivide at a relatively high rate, a telosome for the proper arm may already have been recovered without a special search. One advantage of using the telosome is that it can easily be identified whenever it pairs with its homoe-

ologue, thereby permitting a precise determination of the pairing frequency and the prediction of the resultant frequency with which transfer chromosomes (recombinant chromosomes carrying the specified alien gene) will be produced (about one-fourth of the pairing frequency). A greater advantage of using the telosome is that this facilitates the identification and characterization of the transfer chromosomes. A possible third advantage is that recombination tends to be shifted distally in the telosome as compared with the complete chromosome. Whether or not this shift will be advantageous depends on the location of the alien gene concerned and the distribution pattern of recombination between the alien chromosome and its wheat homoeologue.

With the alien chromosome monotelosomic and its homoeologue monosomic, several types of gamete are produced (Figure 5.5) depending on whether recombination occurs proximal or distal to the gene concerned. Following a cross to euploid, the offspring carrying the alien gene will be of three types: (1) those with the unchanged alien telosome; (2) those with a telosome that has its terminal portion replaced by a wheat segment (as the result of a distal crossover); and (3) those with a wheat chromosome which, as the result of a proximal crossover, has had the distal portion of one of its arms replaced by an alien segment. These are easily distinguished cytologically, for in type 1 the telosome remains unpaired (*Ph1* being present); in type 2 it pairs, with a frequency depending on the length of the terminal wheat segment; and in type 3 the alien gene is present but there is no telosome.

The only experiment thus far completed using an alien telosome (Sears, unpublished) involved a chromosome (called 3Ag) from *Agropyron elongatum* carrying a gene *Lr24* for resistance to the leaf-rust fungus. A previous experiment, in which complete 3Ag and 3D were monosomic, 5B nullisomic, and 5D trisomic (Table 5.2), had given rise to 20 transfers among 299 offspring (Sears, 1972a, 1978). Two of the 20 involved 3B instead of 3D, and one involved both 3B and 3D. The latter was the only one to have resulted from 3Ag-3D exchange distal to *Lr24*. Its terminal 3DL segment was very short, only long enough to support about 3% pairing with 3D. The main reason for undertaking the experiment involving telo-3AgL was the possibility that crossing-over might be shifted distally, as is known to happen with homologously pairing telosomes (Endrizzi and Kohel, 1966; Sears, 1972b).

In the telo-3AgL experiment (Table 5.1) of 328 offspring, eight had transfer chromosomes, one of which was evidently 3B or 3A rather than 3D. Three were 3DL exchanges proximal to *Lr24* (capable of 2%, 11% and 48% pairing, respectively, with telo-3DL). The remaining four were the result of distal exchanges between telo-3AgL and 3DL. Three of the four had very short 3DL segments, none of which was able to support more than about 5% pairing; but the fourth

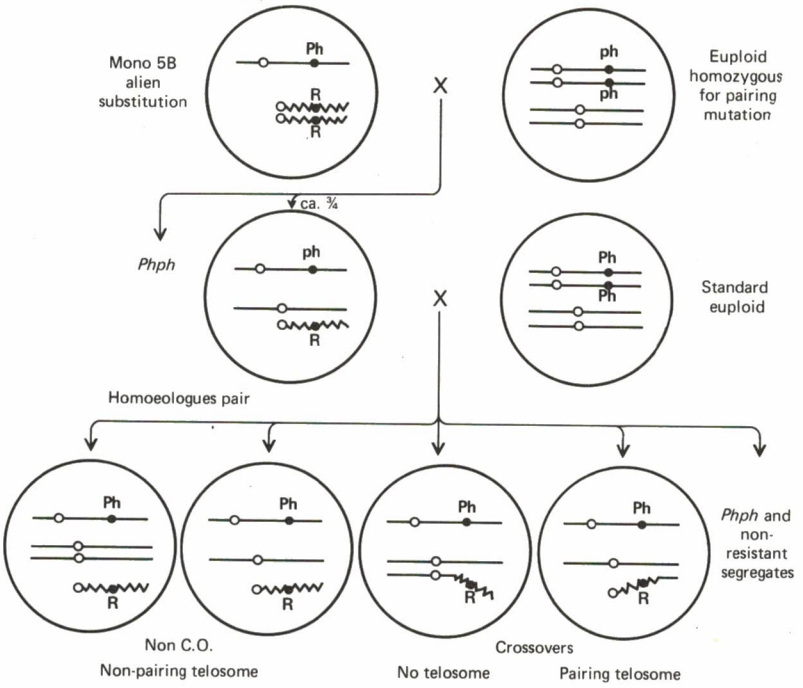

Fig. 5.5. Induction of pairing and crossing-over between an alien telosome and its wheat homoeologue. Each plant has 19 pairs of chromosomes in addition to those shown.

Table 5.2

Comparison of transfers induced from telosome 3AgL with those from the complete 3Ag chromosome

	Type of alien chromosome	
	Telosomic	Complete
Number of plants	328	299
Number with *Lr24*	91	77
Number of proximal transfers	3	17
Number of distal transfers	4	1*
Number not 3D	1	2

*Also had transfer with 3BS

had 28% pairing (in 50 cells). Thus the exchanges involving 3D consisted of 4 distal to *Lr24* and 3 proximal; whereas in the complete-3Ag experiment the corresponding numbers were 1 and 17. The fact that only eight transfers were obtained from telo-3AgL contrasts with the 18 of the previous, slightly smaller experiment and suggests that the increase in distal crossovers does not entirely compensate for the decrease in proximal exchange. This appears to be in contrast to Sallee and Kimber's (1979) finding that the frequency of homologous pairing of wheat telosomes is not significantly reduced, presumably because additional distal chiasmata compensate for the fewer proximal ones. However, the 18 transfer chromosomes include several that may well have an exchange in 3DS rather than 3DL.

In the foregoing experiment, telo-3DL and complete 3Ag might have been used instead of telo-3AgL and complete 3D, but not to as great advantage. Use of 3DL would have permitted scoring of the amount of its pairing with the alien arm; but identification of transfer chromosomes would have been more difficult than when 3AgL was used, mainly because the possible transfer chromosomes could not have been tested immediately for pairing with 3Ag, since combining them with 3Ag would have concealed the presence of *Lr24*.

The desirability of obtaining a transfer chromosome with a 3AgL segment shorter than any of those obtained in either of the two completed experiments is based on the reasoning that the shorter the segment of alien chromatin, the less the danger that one or more deleterious genes will accompany the desirable gene. This is not to deny that other advantageous genes may be present on a particular long, alien segment; in fact, the 3D/3Ag transfers thus far obtained carry a very desirable *Agropyron* stem-rust gene, *Sr24* (McIntosh, personal communication). But, barring prior knowledge of the existence of such additional genes, the cytogeneticist's goal must be to deliver to the breeder a transfer chromosome that includes the shortest possible alien segment.

The fact that one distal-transfer chromosome had 28% pairing with telo-3AgL clearly established that *Lr24* is located a substantial distance from the end of the arm. There was therefore virtually no chance of obtaining a transfer chromosome with a short alien segment in one episode of induced homoeologous pairing. Obtaining a short, interstitial segment requires two crossovers near together, and these are rare even between homologues. They are likely to be even less frequent between homoeologues.

The same result as from such a double crossover can be obtained, however, by combining two transfer chromosomes having exchanges near the gene on the proximal and distal sides, respectively (Figure 5.6). These two chromosomes are homologous only in the segment of alien chromatin they have in common, a region that includes the gene concerned. Every crossover that occurs will give

rise to a chromosome that is entirely of wheat except for an interstitial segment consisting of the region possessed in common by the two parental chromosomes. Thus the closer each of the two original exchanges is to the desired alien gene, the shorter the interstitial segment will be in the derived recombinant chromosome.

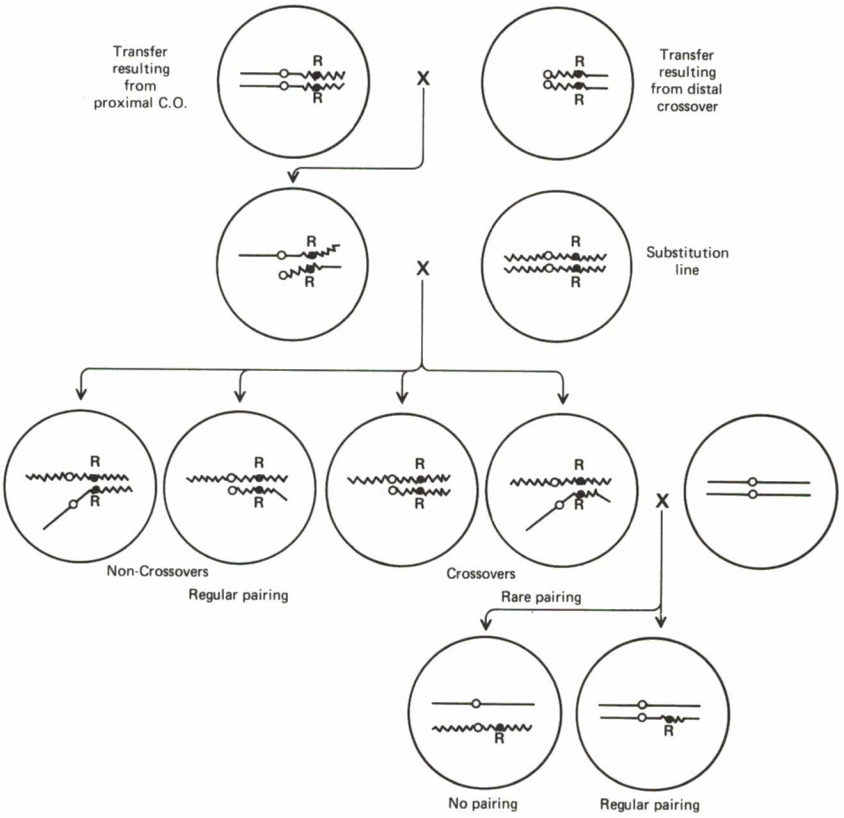

Fig. 5.6. Derivation and identification of a chromosome with a shortened interstitial alien segment from two transfers of different type.

Another possibility for obtaining a transfer chromosome with a short, intercalary alien segment carrying the desired gene is particularly applicable if a reasonably large experiment has yielded only one type of transfer; i.e., involving exchanges either all proximal or all distal to the gene concerned. In such case,

the transfer chromosome with its exchange closest to the gene may be combined with the corresponding all-wheat chromosome in a plant whose genotype permits homoeologous pairing (Figure 5.7). Homoeologous recombination will then presumably occur between the corresponding alien and wheat segments, replacing part of the alien piece with wheat chromatin. Unfortunately, there will be difficulty in identifying the desired recombinants if the parental transfer chromosome already pairs in high frequency with the critical arm of the wheat chromosome.

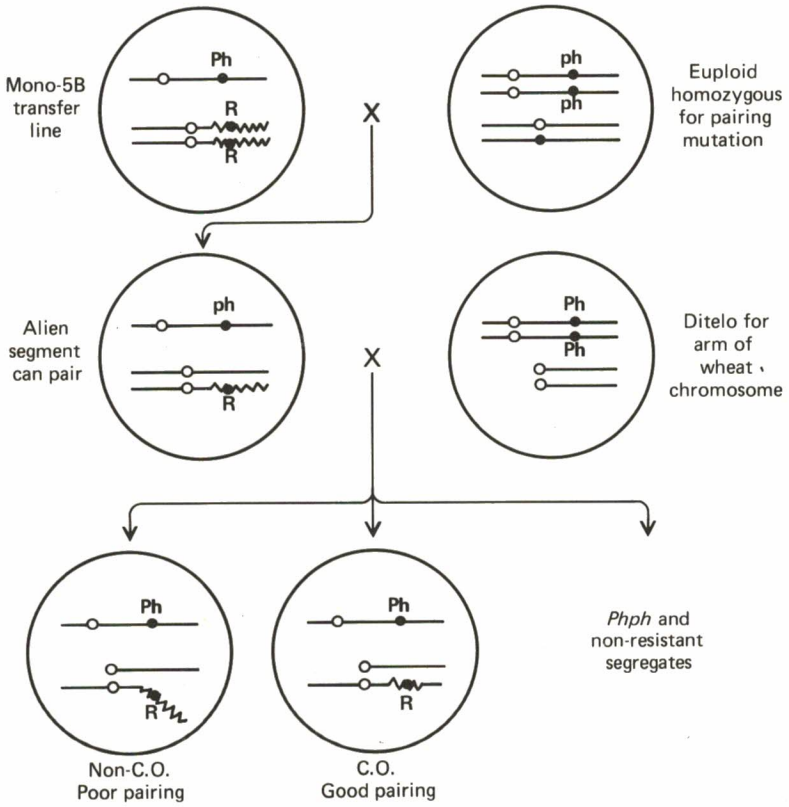

Fig. 5.7. Shortening the alien segment of a transfer chromosome by inducing it to pair homoeologously with the corresponding wheat segment.

If the experiment involving telo-3AgL had been the first attempt to transfer *Lr24* to wheat chromosome 3D, and if no transfer due to proximal recombination had been recovered, this would have signified that the gene was located in

the proximal portion of the arm. An experiment using the complete 3Ag would then have been in order, because this would have tended to move the exchanges proximally. If *Lr24* had been tightly linked to the centromere, an exchange on the other side of the centromere in the short arm would still have been useful. In combination with a suitable exchange distal to *Lr24* in the long arm, it would have given rise to a 3D chromosome with an intercalary *Agropyron* segment carrying *Lr24*. The segment would have included the centromere, but this would presumably not have prevented the chromosome from behaving like any completely wheat chromosome, nor from pairing normally with 3D.

Of the 17 transfers resulting from the experiment involving the complete chromosome 3Ag, the two with the shortest *Agropyron* segment were transfers 3 and 14. Both had a relatively high frequency of pairing with telo-3DL (64% and 69%, respectively), and they are apparently the only transfers that have the *R1* (red seed) locus (which lies proximal to *Lr24*) from 3D instead of 3Ag (McIntosh, personal communication). When each of these two transfers was combined with the highest-pairing distal-transfer chromosome from the telo-3AgL experiment (the chromosome that paired with 3DL in 28% of cells), the segment that this chromosome had in common with transfers 3 and 14 proved to be substantial: enough to result in pairing in 89% of the cells.

The location of *Lr24* in this rather long region cannot be deduced from the available data. Obviously additional transfers must be induced from telo-3AgL. The experiment already performed with telo-3AgL resulted in the recovery of transfers with exchange points that were apparently fairly well distributed along the length of the arm. If a similar distribution occurs in a larger experiment, it is reasonable to expect some transfers with exchange points closer to *Lr24*, unless the segment in which *Lr24* is located is for some reason unable to support chiasmata with the corresponding portion of 3DL. If the desired transfer or transfers are obtained, they will not only locate *Lr24* more precisely but will permit the synthesis of a transfer chromosome with only a short interstitial *Agropyron* segment. In any case, the larger experiment should give a better idea of how nearly random the induced recombination is between 3AgL and 3DL.

Conclusion

Genes can be transferred to the chromosomes of wheat from its relatives by genetic induction of homoeologous pairing in hybrids, or derivatives from hybrids, that have one or more alien chromosomes. This can be done by removing chromosome 5B, on which *Ph1*, the major pairing suppressor, is located; by neutralizing *Ph1* with the genome of *Triticum speltoides* or *T. tripsacoides*; or by using the mutation *ph1b*, which is evidently a deficiency for

the locus. A greater degree of precision can be attained by having present a single alien monosome and a monosome for one of its homoeologues. Having the alien chromosome telosomic facilitates identification and characterization of the transfer chromosomes obtained. By allowing recombination between two transfer chromosomes, one with its exchange point proximal to the alien gene concerned and the other distal, a wheat chromosome with an intercalated alien segment can be produced.

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