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H. Thomas

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Interspecific manipulation of chromosomes

By H. Thomas

Welsh Plant Breeding Station, Plas Gogerddan, Aberystwyth, Dyfed SY23 3EB, U.K.

The success of introducing alien variation into crop species from related species depends on the cytogenetic relations between the species. If there are no restrictions on chromosome pairing and recombination in species hybrids, a backcrossing programme can be used to obtain the desired gene transfers. However, when there is a failure of adequate chromosome pairing in species hybrids, techniques of chromosome manipulation have to be used to obtain alien gene transfers. In polyploid crop species it is possible to introduce appropriate single chromosomes of the alien species into the genotype of the recipient species, but the failure of the alien chromosome to become integrated into the genotype of the recipient species often leads to meiotic instability. The introduction of segments of alien chromosomes has been successful through the use of irradiation-induced translocations. The deletions/duplications that are a consequence of such translocations do limit the usefulness of this approach.

In a number of allopolyploid crop species, regular bivalent pairing behaviour has been shown to be genetically controlled. By interfering with the genetic system controlling the diploid-like pairing it is possible to induce pairing between the alien chromosomes and its corresponding chromosomes in the crop species. Gene transfers based on this method involve exchanges between chromosomes of similar gene sequences.

These techniques are discussed and application of the procedures to transfer alien variation into the cultivated oat is described. A scheme is also proposed for transferring the genes controlling regular bivalent pairing from natural polyploid species into synthetic amphiploids in *Lolium*/*Festuca*.

INTRODUCTION

Crop species often lack desirable characters that are found in related species, e.g. resistance to pests and diseases, and it would be advantageous to introduce these traits into the crop species. If the donor and recipient species are closely related and there is no restriction on chromosome pairing in the interspecific hybrid, the transfer of genes from one species to another can be accomplished by conventional plant breeding methods such as backcrossing.

However, conventional plant breeding methods cannot be employed when the chromosomes of the alien species and the crop species are structurally diverged, or there is a genotypic restriction on chromosome pairing in interspecific hybrids. Failure of corresponding chromosomes to pair at meiosis in the interspecific hybrids results in the absence of recombinants in the derivatives of the hybrids. Backcrossing and selecting for the character being transferred in this situation results in the introduction of whole chromosomes as addition or substitution lines (Riley *et al.* 1966; Sharma & Forsberg 1974; Cameron 1966). To introduce desirable alien variation in these circumstances, procedures of chromosome manipulation have to be followed. The techniques of chromosome manipulation used to transfer alien variation into crop species involve the introduction of a segment of the genome of the donor species. In general, such procedures can only be carried out in polyploid species because the genetic duplication inherent in the structure of such species allows the genotype to tolerate some loss and addition of chromosome material.

The greatest success has been achieved in introducing alien variation into bread wheat. The availability of series of aneuploid stocks (Sears 1952) has been the major contributory factor in establishing procedures of gene transfer in wheat. Aneuploid stocks have been widely used to study the genomic structure of bread wheat and its cytogenetic affinity with related species (Sears 1974). An understanding of these cytogenetic relations has led to the establishment of procedures of gene transfer by chromosome manipulation. Partial series of similar aneuploid stocks have been established in cotton (Endrizzi & Ramsay 1979) and oats (Rajhathy & Thomas 1974), and these will facilitate the use of chromosome manipulation in these crop species.

Chromosome addition lines

O'Mara (1940) proposed that an alternative to combining the complete chromosome complements of two species in synthetic amphiploids, as a means of using alien variation, would be to introduce single chromosomes of the donor species into the genotype of the recipient species. O'Mara (1940) was able to add rye chromosomes, with different phenotypic effects, to the wheat genome by backcrossing the amphiploid between the two species to wheat and selecting addition lines from the progeny of the backcrosses. This method of producing single chromosome addition lines has been successfully used to add single chromosomes of alien species to a range of cultivated species (see review by Lacadena 1978).

The effect of the single alien chromosome on the regularity of chromosome behaviour and fertility is variable, depending on which chromosome of the alien species is added to the cultivated species. The addition of some rye chromosomes to wheat disturbed meiotic behaviour, while others had little effect (Riley 1960). Aberrant meiosis leads to instability in the breeding behaviour of the addition lines. This is well illustrated in the disomic addition line combining the pair of chromosomes of the wild oat species *Avena barbata* ($2n = 28$) on which the gene conferring mildew resistance is located with the complement of the cultivated oat *A. sativa* ($2n = 42$) (Thomas *et al.* 1975). The fertility and agronomic performance of the disomic addition line are satisfactory, but the pair of alien chromosomes fails to synapse in 3% of the pollen mother cells. This partial asynapsis leads to the presence of monosomic addition lines ($2n = 43$) in the progeny of the disomic addition line. The transmission of the *A. barbata* monosome is extremely low, and 90% of the progeny of monosomic addition lines revert to the euploid number, and the agronomic attribute (mildew resistance) of the alien chromosome is lost. A large percentage of the disomic addition line reverts to the original mildew susceptible genotype of *A. sativa* in a few generations. Such instability rules out the commercial exploitation of this chromosome addition line.

In general, chromosome addition lines are not suitable for development as commercial varieties on account of their instability, but they form useful material for starting chromosome substitutions and obtaining induced transfers of alien genes.

Chromosome substitutions

The replacement of a pair of chromosomes by a pair of alien chromosomes can be achieved by crossing a plant monosomic for a particular chromosome with a disomic alien addition line. The F_1 hybrid will be monosomic for the relevant chromosome of the recipient species and the alien chromosome. From the progeny of the hybrid it is possible to isolate disomic substitution lines in which the pair of alien chromosomes has replaced the pair of chromosomes of the recipient species. Alternatively the di-monosomic genotype can be crossed with the disomic addition line to give rise to two different genotypes with $21_{II} + 1_{I}$. One will include 20 pairs plus a monosome of the recipient species and a pair of the alien chromosome. Selfing this plant will yield disomic substitution lines.

If the substitution lines are to be successful the alien chromosome must (1) compensate for the loss of the chromosome of the recipient species, (2) become integrated in the genotype without disturbing meiotic stability and fertility, and (3) confer some agronomic benefit on the crop species.

There are 21 × 7 possible combinations in wheat–rye substitutions, but only the replacement of genetically similar chromosomes (homoeologous) are effective. The alien chromosome has to compensate for the loss of the genetic activity of the replaced chromosome. The seven chromosomes of rye (Koller & Zeller 1976) and *Agropyron elongatum* (Dvořák 1980) can be classified according to their ability to substitute only for the chromosomes of a single homoeologous group in wheat. The ability of the alien chromosome to compensate for the deletion of homoeologous chromosomes of the recipient species is related to their evolutionary derivation from a common chromosome. Differentiation between the chromosomes that has occurred during speciation will be reflected in the effectiveness with which the chromosomes can replace one another in substitution lines. Dvořák (1980) has reported that the extent of compensation observed was variable when the seven chromosomes of *Agropyron elongatum* replace their homoeologous chromosomes in wheat. Substitutions involving homoeologous group seven were as fertile as Chinese Spring, but homoeologous group two substitutions were nearly sterile. Translocations in the alien and recipient species would alter the genetic correspondence of homoeologous chromosomes and hence their compensating ability.

If substitution lines are to be developed into commercial varieties, the alien chromosome must compensate fully for the loss of the pair of chromosomes and give favourable interactions with the rest of the genotype. Wheat cultivars developed in Germany and eastern Europe have been shown to be substitutions of chromosome 1R of rye for 1B of wheat (Zeller 1973; Mettin *et al.* 1973). Triticale was used as a parent in the breeding of these wheat cultivars and selecting for resistance to disease resulted in the spontaneous establishment of these 1R/1B substitutions. The agronomic performance of these cultivars shows that chromosome 1R of rye compensates fully for 1B of wheat and has become integrated into the wheat genotype.

Introduction of segments of alien chromosomes

The introduction of an alien chromosome either as a substitution or addition line often disturbs the genotypic balance of the recipient species, albeit less than the inclusion of the complete complement in amphiploids. In an attempt to avoid the instability caused by the introduction of a complete alien chromosome, procedures for introducing only segments of the alien chromosomes have been established.

Irradiation-induced translocations

Sears (1956) was the first to use irradiation-induced translocations to transfer resistance to brown rust from *Aegilops umbellulata* to bread wheat. The technique relies on chromosomes rejoining in novel combinations after chromosome breakage induced by the irradiation treatment. Sears (1956) irradiated spikes, just before anthesis, of plants with additions of isochromosomes of *Aegilops umbellulata* carrying a gene for resistance to brown rust, and isolated gene transfers in subsequent progeny. Irradiation of dry seeds of the disomic alien addition can also be successfully used to induce translocations (Driscoll & Jensen 1963). In gene transfers based on irradiation-induced translocations there is a deletion of part of the genome of the recipient species and a duplication arising from the alien segment introduced. The usefulness of the gene transfers will depend on the ability of the genotype to tolerate such deletions and duplications.

TABLE 1. SEGREGATION FOR MILDEW RESISTANCE IN THE F_2 FROM BACKCROSS 4 HYBRIDS

(Figures in parentheses are the percentage of susceptible seedlings.)

recurrent parent	resistant	susceptible
Maris Tabard	157	54 (25.6)
Maris Oberon	185	66 (26.3)
Margam	114	50 (30.5)
Maldwyn	98	47 (32.4)
06618 Cn	131	46 (26.0)

A number of putative translocations, involving the transfer of mildew resistance from the wild oat *Avena barbata* ($2n = 28$) to the cultivated oat *Avena sativa* ($2n = 42$), were identified by Aung (1975) after irradiating seeds of the disomic addition line. One of these lines had normal transmission of the translocation, and the euploid plants, including the translocated chromosome, were normal (Aung *et al.* 1977). Aung & Thomas (1978) described the structure of the translocated chromosome as including most of the long arm of the shortest chromosome of *A. sativa* (ST21 according to Rajhathy's numbering system), and the short arm, which carries the gene for mildew resistance, the centromere and a large segment of the long arm of the *A. barbata* chromosome. Although only a small portion of the *A. sativa* genome is deleted, most of the *barbata* chromosome is included in the translocation. The translocation was originally isolated in the cultivar Manod but it has now been introduced into a further five cultivars of oats.

There is clear evidence that the translocation interacts with the genetic background, both at the gametic and zygotic level. When the backcross 4 hybrids were selfed there was a deficiency of resistant progeny in Margam and Maldwyn backgrounds (table 1). This has been shown to be the result of impaired transmission of pollen including the translocated chromosome in competition with haploid pollen in plants heterozygous for the transfer (Aung & Thomas 1978). The transmission of the translocated chromosome is influenced by the genetic background.

Trials to assess the yield potential of the cultivars including the translocation compared with the recipient cultivars have been undertaken by I. T. Jones (personal communication) at the Welsh Plant Breeding Station. Since the original cultivars were susceptible to mildew, they were sprayed with fungicide to eliminate the effect of mildew infection on yield. The advantage of the resistance to mildew conferred by the transfer is nullified by spraying, and it is possible to assess the effect of the translocation on yield in different genotypic backgrounds by comparing the performance of the transfers with the original cultivar. In table 2 the yield of the translocation lines (BC_4) are expressed as the yield of corresponding cultivars. It is clear that the presence of the translocation interacted with the genetic backgrounds. In Maris Tabard the yield of the transfer was equal to the original cultivar while the presence of the translocation significantly depressed yield in Margam. The highest yielding cultivar was the W.P.B.S. selection 06618 Cn and the yield of the transfer was only 3.21 % less than the original cultivar. These results show the importance of assessing such transfers in as wide a range of genetic background as possible in a breeding programme. Intercrossing the different cultivars, which are homozygous for the translocations, will give further opportunity for selecting more favourable genetic backgrounds without having to select for resistance to mildew. The advantage of the incorporation of the mildew resistance is shown in the comparison between the yield of the transfers and the original cultivars when the latter were not sprayed (table 2).

TABLE 2. YIELD OF TRANSLOCATION LINES IN DIFFERENT GENETIC BACKGROUNDS (BACKCROSS 4)

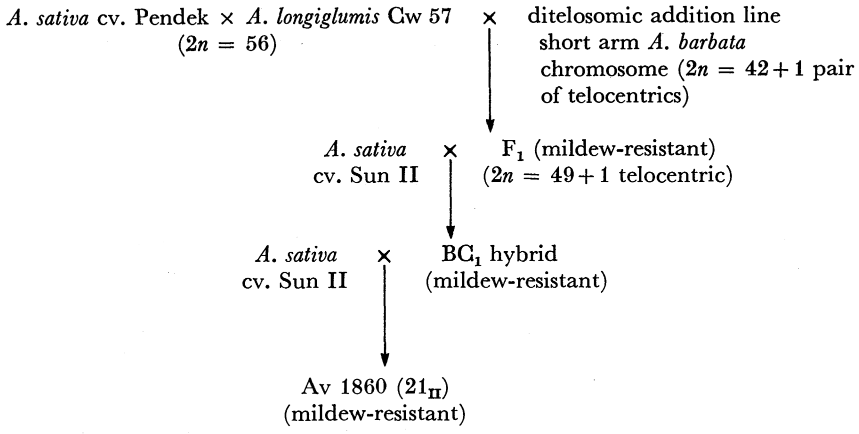
	yield of translocation line	
recurrent spray	as percentage of original cultivar sprayed	as percentage of original cultivar unsprayed
Maldwyn	93.48	102.70
Margam	78.18	83.41
Maris Tabard	100.85	108.38
06618 Cn	96.79	102.48
Maris Oberon	91.12	94.75

Knott (1968) and Dvořák & Knott (1977) have demonstrated that a number of transfers of *Agropyron* genes into wheat based on induced translocations are exchanges between homoeologous chromosomes. Selection for regular transmission has led to the isolation of transfers in which the deletion of the recipient wheat chromosome is compensated for by a segment of the homoeologous *Agropyron* chromosome. In the *Avena* transfer, the *A. barbata* and *A. sativa* chromosomes involved in the translocation were not homoeologous (Aung & Thomas 1978). Transec, a wheat–rye irradiation-induced translocation, has also been shown to be an exchange between non-homoeologous chromosomes by Driscoll & Anderson (1967). In these translocations the loss of a small portion of the genome of the recipient species is tolerated.

GENETIC-INDUCED GENE TRANSFERS

The failure of alien chromosomes to pair with their corresponding chromosomes in the cultivated species is not always associated with structural differentiation of the chromosomes but with the genetic control of chromosome pairing. In wheat, regular bivalent pairing is controlled by the *Ph* gene on the long arm of chromosome 5B (Riley & Chapman 1958; Sears & Okomota 1958). The *Ph* gene restricts pairing to homologous chromosomes and the homoeologues of the three constituent genomes synapse and form chiasmata associations only when chromosome 5B is deleted. The presence of such a genetic system in natural allopolyploids is also responsible for minimizing pairing between alien chromosomes and their homoeologues in the crop species. The relaxation of the control mechanism leads to pairing between alien chromosomes and the corresponding wheat chromosomes (Riley & Chapman 1963; Dvořák & Knott 1972). By manipulating the control mechanism to allow homoeologous chromosomes to pair, Riley *et al.* (1968) and Sears (1973, 1978) have been able to induce alien chromosomes to pair with their homoeologues in wheat and isolate recombinants including genes located on the alien chromosome. Riley *et al.* (1968) used genotypes of *Aegilops speltoides*, which suppresses the activity of the *Ph* gene, while Sears (1973), using the appropriate aneuploid lines, deleted chromosome 5B to induce pairing between alien chromosomes and their homoeologues in wheat.

TABLE 3. THE CROSSING SCHEME USED TO ISOLATE GENETICALLY INDUCED TRANSFER OF MILDEW RESISTANCE FROM *A. BARBATA* TO THE CULTIVATED OAT



The techniques were developed by wheat cytogeneticists based on their understanding of the genomic structure and meiotic behaviour of wheat and its related species. There is strong evidence that regular bivalent pairing in *Avena sativa* is also genetically controlled, although the precise chromosome or chromosomes carrying the effective genes have not been definitely identified (Rajhathy & Thomas 1974). A genotype of the diploid species *A. longiglumis* (Cw 57) has been reported to modify the genetic mechanism controlling bivalent pairing in *A. sativa* and induce homoeologous chromosome pairing (Rajhathy & Thomas 1972; Thomas & Al-Ansari 1980) in a manner comparable to *Aegilops speltoides* in wheat.

The effect of the *A. longiglumis* (Cw 57) has been successfully used to transfer mildew resistance from *A. barbata* to the cultivated oat (Thomas *et al.* 1980). The crossing scheme is represented in table 3. The identification of progeny resistant to mildew (Av 1860), in which the telocentric is absent, is proof of crossing over between the *A. barbata* and *A. sativa* chromosomes. In hybrids between *A. sativa* and Av 1860, 21 bivalents were regularly formed. In the absence of the Cw 57 genotype, no natural recombinants were recovered from the progeny of the monosomic addition line (Thomas *et al.* 1975). The isolation of recombinants is attributable to the induced pairing of homoeologous chromosomes in the presence of the Cw 57 genotype.

In contrast to irradiation-induced translocations, all exchanges in genetic-induced transfers are between homoeologous chromosomes. The introduced segment of the alien chromosome replaces a segment of a genetically equivalent chromosome of the recipient species. In view of the evolutionary derivation of the chromosomes from a common chromosome, the segment of the alien chromosome has a good chance of compensating fully for the segment of the chromosome of the recipient species replaced. The degree of compensation will depend on how close the gene order has been conserved in the alien and homoeologous chromosomes during evolution. Sears (1973, 1978) has reported variation in the transmission of a number of wheat–*Agropyron* transfers, which reflect such differences.

When the introduction of alien genes is dependent on recombination as a result of the suppression of the control mechanism, there are better opportunities for restricting the size of the segment of the alien chromosome incorporated. In the *Agropyron* transfers described by Sears (1978) there was variation in the size of the segment of the alien chromosome introduced. The ability to isolate transfers based on smaller segments of the alien chromosome improves the chances of breaking undesirable linkages found in whole chromosome substitution and additions. Genetically induced chromosome pairing introduces greater precision as a method of gene transfer than irradiation-induced translocations. However, irradiation remains a valuable technique when the alien chromosomes fail to synapse with related chromosomes in the crop species on account of structural differentiation.

In situations where the alien chromosome fails to pair even when homoeologous pairing is induced, Sears (1972) proposed a method based on fusion of telocentric arms. In plants monosomic for an alien and a recipient species chromosome, misdivision of the univalents and union of the resulting telocentric would give rise to a chromosome including an arm from both univalents. If the two chromosomes concerned were homoeologous there would be a good chance of compensation, but in the event of fusion between arms of non-homoeologous chromosomes, success would depend on the ability of the genotype to tolerate the deletion and duplication. Sears (1972) has produced wheat–rye translocations by using this method.

Procedures to transfer alien variation into crop species have been developed to overcome barriers that have arisen during speciation to prevent gene flow and recombination. Stable meiotic behaviour in natural allopolyploids is ensured by the restriction of pairing to homologous chromosomes. The presence of such genetic systems has maintained the integrity of the constituent genomes during evolution. The development of commercial varieties based on synthetic amphiploids combining diploid genomes has often been hampered by irregular meiotic behaviour including allosyndetic pairing, which leads to the dissipation of advantageous gene combinations. If the genetic system in natural allopolyploids could be transferred into synthetic polyploids it should stabilize the meiotic behaviour of the newly synthesized allopolyploids.

The natural allopolyploid *Festuca arundinacea* ($2n = 6x = 42$) has regular bivalent pairing and disomic inheritance (Lewis *et al.* 1980), two features of homogenetic pairing in allopolyploids. Jauhar (1975) proposed that the restriction of chromosome pairing to homologous pairs is controlled by a gene or genes that are ineffective in the hemizygous conditions. Data on chromosome pairing between natural bivalent-pairing tetraploid and hexaploid species of *Festuca* produced by M. Borrill and W. G. Morgan at this station also show evidence of the genetic control of chromosome pairing in these polyploid species. In euhaploids and interspecific hybrids with diploid species of *Festuca* and *Lolium*, the control system does not operate and allosyndetic pairing occurs freely. It should therefore be possible to isolate recombinants, including the *F. arundinacea* pairing genes in *Lolium* genotypes. We are now attempting to establish such gene transfers at this station and use them to improve the regularity of meiotic behaviour and the stability of tetraploid hybrid combinations involving *Lolium* species. Since there is a tendency to preferential pairing in *L. perenne* × *L. multiflorum* synthetic tetraploids (Lewis 1980), the inclusion of the pairing genes in the disomic condition should further enhance preferential pairing and the stability of the amphiploids.

Further refinements of techniques of chromosome manipulation for the transfer of alien genes into crop species will probably be concerned with reducing the size of the segment of the alien chromosome introduced in such transfers and consequently the chances of introducing any undesirable linked genes. Pandey (1978, 1980) has described the introduction of single genes in *Nicotiana* by using pollen that had been treated with a large dose of ionizing radiation. Segments of DNA from the treated pollen are incorporated into the egg of the recipient species and the 'genetically transformed' egg developed parthenogenetically into a viable seed. More information is required on the mechanisms involved in the transformation of the egg and the doubling of the chromosome number of the egg leading to normal seed development before the wider application of the technique can be evaluated.

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