

II.1 Wide Hybridization – Potential of Alien Genetic Transfers for *Triticum aestivum* Improvement

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1 Introduction

In the Triticeae, hybridization of alien species with those of *Triticum* goes back to 1876 when Wilson consciously made the first wide hybrid involving wheat and rye. Rimpau in 1891 obtained seed on a presumably doubled sector in a wheat × rye hybrid and described 12 plants that must represent the first triticale. A more divergent hybrid (wheat × barley) was first reported by Farrer in 1904 that was considered rather improbable to be a true hybrid (Shepherd and Islam 1981).

Many hybrids involving *Triticum* and *Aegilops* species were produced during the 1920's and 1930's (Kihara 1937) from which the genomic relationships of the genus were derived (Lilienfeld 1951). Subsequently, the pioneering work of the late Anton Kruse in attempted hybridization with *T. aestivum* × *Avena sativa* (Kruse 1969), *Hordeum vulgare* × *Secale cereale* (Kruse 1967), and *H. vulgare* × *T. aestivum* (Kruse 1973) led to an increase in research momentum in the area of intergeneric hybridization involving *T. aestivum* or *T. turgidum* with species of *Agropyron*, *Aegilops*, *Elymus*, *Haynaldia*, *Heterantheium*, or *Hordeum*, an intensity that has magnified over the last decade and a half. These hybridization projects either had practical motivation or they aimed at providing basic information as related to cytology, evolution, or phylogeny of the parental species involved in forming the hybrid.

The genera discussed here are treated in their traditional sense as used predominantly in the present literature except where genome crossability barriers are discussed. It is recognized, however, that based upon genome relationships, Dewey (1982, 1984), after Tzvelev (1976), proposed a taxonomic revision of the genus *Agropyron*. Dvorak (1981a,b) adopts a new nomenclature that varies significantly from this revision. The genomes identified in the *Agropyron* species complex are S, E, Ju, C, J, H, X, and Y (Stebbins and Pun 1953; Stebbins 1956; Sakamoto 1966, 1973; Dewey 1982, 1984). The diploid genome donors are *A. spicatum* (S), *A. elongatum* (E), *A. junceum* (Ju), *A. cristatum* (C), *Elymus junceus* (J), and *H. bogdanii* (H), with X and Y being genomes of unknown origin. Of the 325 species in the Triticeae approximately 250 are perennials (Dewey 1984) and relatively few of these are hybridized with wheat. However, over the last decade phenomenal success has been achieved in the production of complex hybrids amongst the Triticeae, leading to a potential stock of valuable alien genetic material introduced from wide hybrids.

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These combinations are reported and/or reviewed in detail by Dewey (1984), Sharma and Baenziger (1986), Sharma and Gill (1983a,b,c), Mujeeb-Kazi and Kimber (1985), Mujeeb-Kazi et al. (1987, 1989; see also Chap. II.4, this Vol.). The major problems limiting hybrid production and exploiting alien genetic variability common in the above reports, and also of prime importance for several other researchers are associated with crossability barriers plus hybrid embryo development. Success in lowering crossability barriers and improving embryo development should logically extend the range of wide hybrid production to include not only more species of a genera but even unique genera like *Taeniantherum*, *Henrardia*, *Zea mays*, and *Sorghum*. The value of conserving alien germplasm is extremely high and the prevalent genetic diversity has significant value in unraveling unique genes for wheat improvement that otherwise may be inaccessible for conventional crop improvement. This chapter elucidates the methodology, techniques, and novel approaches, and identifies certain constraints in the use of alien germplasm for wheat improvement, but in general it is our intention to highlight the enormous potential of wide crosses in the cereals.

2 Hybrid Production

The production of the earliest intergeneric hybrids was accomplished by the simplest techniques of emasculation and pollination as commonly utilized in conventional wheat breeding programs, and it is presumably safe to conclude that the easiest hybrid combinations were earlier also made by these procedures. A wide hybrid production procedure in which wheat is the maternal parent is routinely adopted with significant success (Mujeeb-Kazi et al. 1987). The procedure involves early or bud pollinations, post-pollination gibberellic acid treatment (75 ppm aqueous) of the maternal floret tissue up to 4 days, embryo excision from 14 to 18 days post-pollination, embryo culture on Murashige and Skoog's (1962) or Taira and Larter's (1978) media, cold treatment to break dormancy, and eventually culminates in plantlet differentiation. Despite this protocol, hybridization success is limited and an array of manipulative techniques becomes essential in order to obtain viable hybrids. These range from pre-pollination to post-pollination hormonal treatments. Genotypes, polyploidy level, crossing procedure, and cross direction all seem to contribute to hybrid production success (Mujeeb-Kazi and Kimber 1985; Sharma and Gill 1983a). Most intergeneric hybrids in the Triticeae have been predominantly produced with the *T. aestivum* cultivar Chinese Spring. The highly successful role of Chinese Spring is attributed to the $kr_1kr_1kr_2kr_2kr_3kr_3$ crossability genes it possesses (Falk and Kasha 1981; Fedak and Jui 1982) for its crossability with rye (Riley and Chapman 1967). The loci are located on chromosomes of homoeologous group 5 in kr_1 (5B), kr_2 (5A), kr_3 (5D) respectively and act in a complementary manner, with the kr_1kr_1 loci contributing most to the crossability frequencies.

A minor role in crossability success may also be assigned to the alien species as elucidated in wheat × barley crosses, i.e., *H. vulgare*, *H. chilensis*, *H. bogdanii*, or *H. bulbosum*. Additional evidence is supportive of the better combining ability of the

cultivars of an alien species, i.e., Betzes or Manker of *H. vulgare* (Thomas et al. 1977). Early or bud pollinations have an advantage over the conventional pollination timings, particularly for those combinations where embryo recovery frequencies are low. In future, it is anticipated that bud pollinations may contribute as one significant variable in producing difficult to obtain hybrids between *T. aestivum* and the alien species.

In several cases reciprocal crosses (alien species \times *T. aestivum*) may be the only way to combine the alien species with wheat. Some species that fit this category include the following: *A. caninum* (Sharma and Baenziger 1986); *A. ciliare**; *A. fibrosum*+; *A. scabrifolium*+; *A. scabriglume*+; *A. trachycaulum**+; *A. yezoense**; *E. canadensis*+; *E. virginicus*+; *E. agropyroides*+, and *E. dahuricus*+ (* = Sharma and Gill 1983a; + = Mujeeb-Kazi and Bernard 1985a). Although the uniqueness of developing alloplasmic germplasm exist, constraints also prevail where empty pollen mother cells in the F_1 hybrid render genomic evaluation impossible (*A. scabriglume* \times *T. turgidum*) or advanced backcross derivatives upon selfing remain sterile. The latter situation is exemplified by the *H. vulgare* \times *T. aestivum* cross combination (Islam et al. 1975, 1978; Mujeeb-Kazi and Rodriguez 1983a,b, 1984).

Bridge crossing may be another approach to overcome crossability barriers where the F_1 hybrid or the pollen parent may facilitate hybridization with *T. aestivum*. Two examples are provided to which several others with permutations can be added. The direct *T. aestivum* \times *Heteranthelium* sp. cross remains unsuccessful but a *Heteranthelium* sp. \times *A. elongatum* hybrid was produced that now may presumably be successfully top-crossed with *T. aestivum*. Similarly, the *T. aestivum* \times *A. desertorum* cross failed consistently but crossing *T. aestivum* with the amphiploid of *A. repens* \times *A. desertorum* ($2n = 10x = 70$) produced several hybrids with a $n = 8x = 56$ chromosome complement (Mujeeb-Kazi et al. 1989).

The contribution of polyploidy in overcoming crossability barriers in the Triticeae is exemplified by crosses of natural or induced auto-tetraploids of *A. cristatum* and *E. junceus* with *T. aestivum*. Alien diploids are preferred in wide hybridization but are generally difficult to hybridize with wheat. There is merit in either inducing autotetraploidy or using natural auto-tetraploids as pollen parents where F_1 hybrids with wheat have 35 chromosomes and are genomically ABDJJ (*T. aestivum* \times *E. junceus*). When this F_1 is backcrossed by wheat there is an added advantage in that the backcross I seed is also an amphiploid (Fig. 1).

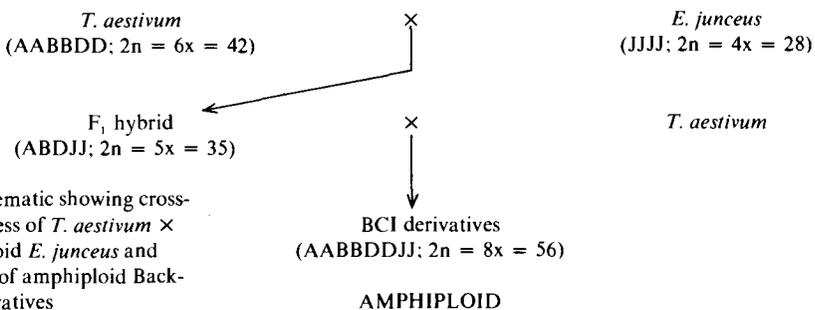


Fig. 1. Schematic showing crossability success of *T. aestivum* \times autotetraploid *E. junceus* and production of amphiploid Backcross I derivatives

3 Cytology of Hybrids

Initial hybrid identification is based upon mitotic counts in root tips collected at various hybrid development stages (Mujeeb-Kazi and Miranda 1985). A normal intergeneric F_1 hybrid possesses half the chromosome number of each parent involved in the combination. For hybrids of different polyploidy levels a mere number count is adequate initial verification. There are, however, cases where the alien species are hexaploid, like wheat, and hybrids would then have 42 chromosomes. These may be difficult to classify categorically as hybrids but with superb primary and secondary constriction resolution of wheat 1B, 6B, 5D chromosomes (Mujeeb-Kazi and Miranda 1985), identification of hexaploid hybrids is simplistic. Additional identification can be made by employing chromosome banding techniques. Karyotypic differences play a part, but positive claim to hybridity must be accompanied by clear meiotic analyses. This permits breeding strategies for each wide hybrid combination to be formulated by metaphase I meiotic data analyses, thus providing a basis for the logical introduction of variation (Kimber 1984). Meiotic cytological data enable genomic analyses and provide a practical base for advancing the F_1 hybrids through the numerical methods of assessing genomic affinity (Kimber and Hulse 1978; Kimber et al. 1981; Alonso and Kimber 1981; Kimber and Alonso 1981; Espinasse and Kimber 1981). When the mean chromosome arm-pairing frequency and the relative affinity have values approaching 1, the alien transfer can be made by recombination. At intermediate values of mean arm-pairing frequency, increased homoeologous pairing can be induced by changes in the system regulating chromosome pairing. At very low values of the mean arm-pairing frequency, irrespective of the value of the relative affinity, irradiation or centric break-and-fusion in derived aneuploids is the optimal method (Kimber 1984).

In some situations the alien genome may be totally or partially eliminated, resulting in the production of polyhaploid/haploid or aneuploid F_1 hybrids. The two aspects are classified under (1) genome elimination, (2) aneuploid F_1 hybrids, and are discussed accordingly.

3.1 Genome Elimination

The phenomenon of genome elimination following hybridization has been observed in a number of intergeneric hybrids involving the Triticeae; namely in *Hordeum* × *Triticum* (Kruse 1974), *Triticum* × *Hordeum* (Fedak 1980; Finch and Bennett 1980; Islam et al. 1981), *Hordeum* × *Secale* (Kruse 1967; Fedak 1977a), *Triticum* × *Elymus* (Mujeeb-Kazi and Bernard 1985b), *Agropyron* × *Triticum* (Mujeeb-Kazi and Bernard 1982), *T. aestivum* × *Zea mays* (Laurie and Bennett 1986) and *Triticum* × *Agropyron* (Mujeeb-Kazi unpubl.). Such an elimination process is a source of valuable cytogenetic information, as it affects genomic relationships in polyhaploid derivatives and at the same time, imparts practicality to wheat breeding in situations where *T. aestivum* polyhaploids result from crosses of *T. aestivum* × *H. bulbosum* (Barclay 1975) or *T. aestivum* × *Z. mays* (Laurie and Bennett 1986) by decreasing the generations required to achieve homozygosity. The

former procedure has also been used in disomic addition line production in wheat \times barley advanced derivatives when a wheat polyhaploid with a mono-alien chromosome was doubled to yield the alien disomic addition (Islam et al. 1981).

3.2 Aneuploid F_1 Progeny

Reports of the occurrence of aneuploid F_1 progeny from intergeneric hybridizations involving the Triticeae are restricted to crosses between *T. aestivum* and *H. vulgare* (Islam et al. 1981). Meiotic instability within complete F_1 hybrids has, however, been more widely reported, e.g., *Triticum* \times *Hordeum* reciprocal hybrids (Fedak 1977b, 1980; Islam et al. 1981; Mujeeb-Kazi and Rodriguez 1983a,b) and within *Hordeum* \times *Secale* hybrids (Finch and Bennett 1980).

4 Utilization of Intergeneric Hybrids: Practicality

In wide crosses classically the self-sterile F_1 hybrids, on colchicine treatment, result in fertile amphiploids that may then have practical utility. \times *Triticosecale* (Wittmack) is the best example of such a process both at the hexaploid or octoploid polyploidy level aided by subsequent breeding improvements. In other cases, the fertile amphiploids are sources of backcross I (BCI) derivatives (amphiploid/*Triticum* source) with eventual production of alien disomic addition lines leading to subtle alien genetic transfers by subsequent cytogenetic manipulation. The method of F_1 hybrid advance under those circumstances where amphiploids are not produced is by pollinating the F_1 hybrid by *T. aestivum* and attaining the crucial BCI advanced derivative. This BCI derivative may be of the classical type where the BC parent is the same as that involved in the F_1 hybrid pedigree (Fig. 2A). There are modifications to this conventional process in that different wheat cultivars than that present in the F_1 hybrid are pollen parents in F_1 hybrids advanced cross progeny (Fig. 2B, C). This process could also be applied when backcross derivatives are to be produced from the amphiploid. A uniform wheat background (Fig. 2A) is advantageous for morphological or biochemical marker applications, but since Chinese Spring is the wheat cultivar most commonly involved in intergeneric crosses, the disomic additions in its background are of little immediate practical value. Top-crossing with a different wheat several times (n^*) as in Fig. 2B with Pavon 76 and a final selfing finishes the addition lines in a commercial wheat background that is readily manageable under the additional necessary field conditions. When two different but not too divergent wheat cultivars are involved

Fig. 2. Schematic showing three approaches of alien addition line production (n^* : several backcrosses to wheat cultivar. \textcircled{n} several selfings of the advanced backcross derivative)

T. aestivum cv. Chinese spring/*Agropyron scirpeum*

A CS/*A. scirpeum*/ / n' CS \textcircled{n}

B CS/*A. scirpeum*/ / n' Pavon 76 \textcircled{n}

C CS/*A. scirpeum*/ / Pavon 76/3/Ciano 79 \textcircled{n}

in top crosses, the resulting progeny simulates the F_1 top cross process of the conventional breeding program. The material at this stage is amenable for field testing, has an excellent segregation differential, and retains adequate alien chromosomes for subsequent controlled manipulation.

It is expected that BCI derivatives from amphiploids/*T. aestivum* would be normal, i.e., normal wheat and normal alien chromosome complements, the former in a double dosage and the latter in a single dosage. However, when a F_1 is crossed by wheat BCI derivatives are produced, although in a low frequency. This occurs via fusion of the wheat pollen with an unreduced egg cell of the F_1 hybrid. This procedure is rapid and meets the research goals but is beset with considerable aneuploidy that is contributed maternally. The unreduced egg cell could be an assemblage of wheat/wheat, wheat/alien or alien/alien translocations and may have drastic aneuploid changes expressed as hyper- or hypoploid progeny in the resulting derivatives (Jewell and Mujeeb-Kazi 1982; Mujeeb and Bernard 1982).

Irrespective of the wheat cultivars used in advancing the F_1 hybrids the derivatives are now referred to as BCI that may be normal or aneuploid. However, if a substantial number of BCI derivatives are obtained, the chances of cytological normalcy are higher. Aneuploidy in BCI is independent of alien genomic constitution, e.g., tending to be minimum in *T. aestivum*/*A. junceum* ($2\times$)//*T. aestivum* with 21 bivalents + 7 univalents and maximized for *T. aestivum*/*A. elongatum* ($10\times$)//*T. aestivum* or *T. aestivum*/*Aegilops variabilis*//*T. aestivum* combinations, where no normal 77 and 56 chromosome BCI derivatives were obtained.

Backcross I derivatives may be self-fertile but in general where a diploid alien species or an alien polyploid with dissimilar genomes is involved BCI plants are self-sterile. Self-fertility of BCI derivatives could be a consequence of complete or partial synthetic genomes that is rampant in intergeneric hybrids of *T. aestivum* with *A. curvifolium*, *A. scirpeum*, *A. junceum* ($4x$), the *A. intermedium* complex including *acutum*, *pulcherrimum*, *trichophorum*, and *varnense*. The self-fertility phenomenon in the three partial autopolyploids (*A. curvifolium*, *A. scirpeum*, *A. junceum* $4x$) is indicative of a genomic composition that may provide novel options for plant level genetic manipulation. Repeated selfings of the BCI derivatives may lead to synthetic genome formation; a means of aggregating complex polygenic recessive traits in a modified package (Mujeeb-Kazi and Miranda 1984). Following repeated selfings of the BCI, additional backcrosses intermingled with cytology lead to the production of addition lines that we contend will be different from those where the BCI is directly advanced to BCII, BCIII etc., and yield addition lines (Fig. 3). Other tetraploids that could be evaluated for complete synthetic genome possibilities are *A. distichum* (Pienaar et al. 1977); *A. rechingeri*, *A. scythicum* and the 35 chromosome F_1 hybrid of *A. repens*/*A. desertorum* with *T. aestivum* (Mujeeb-Kazi et al. 1987, 1989).

Partial synthetic genomes are predominantly derived from segmental allohexaploids or autoallohexaploids which possess two similar genomes and a dissimilar third genome. BCI hybrid derivatives possess 42 wheat chromosomes and 21 of the allohexaploid or autoallohexaploid alien. The BCI derivatives are self-fertile, and result in 56 or near 56 chromosome selfed derivatives as a consequence of the complete AABBDD wheat genomes plus the nearly similar E_1E_2 alien

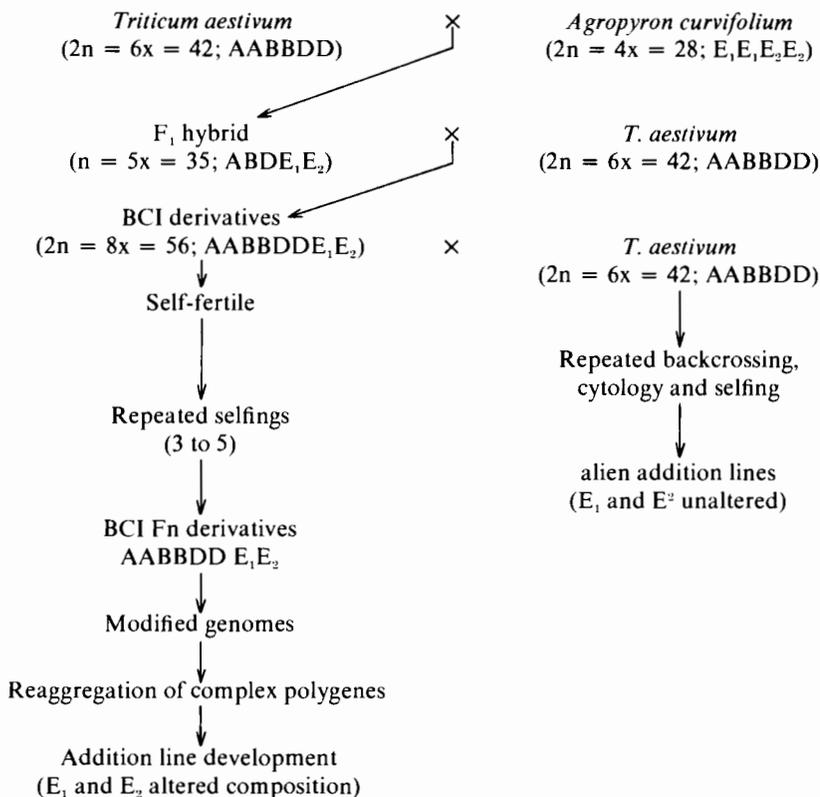


Fig. 3. Synthetic genome development in *Triticum aestivum* × *Agropyron curvifolium* via backcross I production. The modified genomic pathway on the *left* sequence of events leading to addition line development for which the *right* pathway serves as a control

genomes following elimination on selfing of the unrelated third hexaploid genomes. This is thus categorized as partial synthetic genome development, a phenomenon applicable to *A. junceum-mediterraneum*, *A. podperae*, *A. intermedium*, *A. acutum*, *A. pulcherrimum*, *A. trichophorum*, and *A. varnense* (Mujeeb-Kazi and Miranda 1984).

In hybrids of *T. aestivum* with the diploid *A. junceum* addition line development can be conducted by conventional procedures, i.e., F₁ hybrid → fertile amphiploid → BC derivatives → disomic alien additions (Wyn Jones et al. 1986). The self-fertility of the BCI derivatives was surprising, particularly because of the high chromosome number in the selfed progeny of the BCI plants to which *A. junceum* chromosomes contributed uniquely (Table 1). BCIF₁ plants with 49 chromosomes were not uncommon, with these plants exhibiting interesting chromosomal relationships following meiotic analyses, e.g., a 49-chromosome plant with 23 bivalents and 3 univalents. This BCI derivative self-fertility is indeed a fortuitous event and may result in many stable alien disomic derivatives of variable constitutions that

Table 1. Backcross I self-fertile (BC₁F₁) progeny derivation from a *Triticum aestivum* × *Agropyron junceum*-based hybrid combination topped by *T. aestivum* cultivars Genaro 81 and Pavon 76

| Greenhouse plant no. | Cross combination | BCI Chromosome number | No. of spikes harvested | Total seed number |
|----------------------|---|-----------------------|-------------------------|-------------------|
| 2388 | CS ^a / <i>A. junceum</i> (2×) ^b // Genaro 0 | 48(2t) ^c | 4 | 71 |
| 2389 | " | 48 | 8 | 123 |
| 2390 | " | 49 | 4 | 129 |
| 2391 | " | 49 | 6 | 28 |
| 2392 | " | 48 | 4 | 146 |
| 2393 | " | 49 | 7 | 77 |
| 2394 | " | 49 | 6 | 102 |
| 2395 | " | 47 | 6 | 25 |
| 2396 | " | 49 | 4 | 43 |
| 2397 | " | 49 | 3 | 85 |
| 2398 | " | 49 | 4 | 112 |
| 2399 | " | 49(2t) | 4 | 104 |
| 2400 | " | 48(t) | 3 | 35 |
| 2401 | CS ^a / <i>A. junceum</i> (2×) // Pavon 0 | 49 | 6 | 141 |
| 2402 | " | 48 | 4 | 12 |
| 2403 | " | 49 | 4 | 79 |
| 2404 | " | 45(t) | 2 | 49 |
| 2405 | " | 49 | 3 | 87 |
| 2406 | " | 48 | 3 | 27 |
| 2407 | " | 49 | 5 | 65 |

^a Chinese Spring.

^b Also *Thinopyrum bessarabicum*.

^c Telocentric chromosome.

qualify for a form of the “partial” amphiploid category. Natural synthesis of such “partial” amphiploids may place together chromosomes with complex major polygenes in mixed disomics, and is worth exploiting.

5 Implications of Alien Genetic Transfers

Production of intergeneric hybrids is only the first step in a series of complex stages that deal with alien genetic transfers leading to improved *T. aestivum* germplasm. Direct gene incorporation from the alien species is not to be anticipated, since most of the F₁ intergeneric hybrids are low recombination types with meiotic pairing to be interpreted as autosyndetic. In alien genetic transfers, so far only rather simply inherited traits have been introgressed (Dewey 1984) and the transfer of complex recessive polygenic characters by wide hybridization is, and may remain, a major limitation. There is of course the remote possibility of observing major gene influences in a polygenic system that consequently may be relatively a simple genetically controlled mechanism. Another significant prerequisite for the success of intergeneric hybrids is the requirement that the significant alien gene(s) is epistatic to the wheat genetic system. The low pairing in F₁ can be manipulated,

polygenic systems can be made more amenable, as demonstrated earlier, by complete or partially synthetic genomes or partial amphiploids, with epistatic expression assessed at the F₁ or BCI stage. Aspects related to gene transfer manipulations, that hold high priority and involve the chromosome 5B mechanism, are briefly presented here.

6 Chromosome 5B Mechanism

There seems to be no parallel to the chromosome 5B-like manipulative approach that encompasses mono-5B, *PhPh* mutant or nulli-tetrasomic stocks as the maternal wheat sources in wide crosses. These stocks enhance wheat/alien recombinations in the F₁ hybrids and all involve the *Ph* system (Sharma and Gill 1983a,b,c; Darvey 1984; Mujeeb-Kazi et al. 1984; Forster and Miller 1985; Sharma and Baenziger 1986). The resultant F₁ hybrids exhibit a high meiotic chromosome pairing frequency but obtaining backcross derivatives was considered to be a major problem. Sharma and Gill 1986 encountered similar constraints when *T. aestivum* × *Aegilops* species hybrids were produced. Subsequently, Ter-Kuile et al. (1987) reported success with the *Ph* maternal system using *T. aestivum* × *Ae. variabilis* as the test cross. Since then, numerous *Ph* manipulative high pairing F₁ hybrids have been routinely produced and advanced to BCI or BCII (Rosas et al. 1988). However, as an alternative, since a general constraint prevails, it may be appropriate to produce the F₁ hybrid with a highly crossable wheat and either back- or top-cross it with the *PhPh* mutant stock (Sharma and Gill 1986). Additional options for influencing the *PhPh* locus are associated with this locus being suppressed by *Ae. mutica* or *Ae. speltoides*; a procedure that could be incorporated at the F₁ stage with low recombination hybrid or on desired alien disomic addition lines. Achieving high recombination is emphasized primarily because the *T. aestivum* crop species with its phenomenal cytogenetic flexibility via *Ph* manipulation offers remarkable opportunities for alien gene transfers and incorporation of homoeologous segments introduced in the best location in the recipient wheat chromosomes.

Some other novel systems for genetic manipulation in intergeneric hybridization have lower research priority than the *Ph*-mediated transfers, but they have either had a tremendous agricultural impact or led to germplasm whose potential has yet to be tapped.

7 Spontaneous and Induced Translocations

Translocations have contributed significantly to disease resistance transfers (Sharma and Gill 1983a) with major impact so far being from the 1A/1R and 1B/1R translocations, presumably greater for the 1B/1R as it influences *T. aestivum* cultivar yields over this decade (Rajaram et al. 1983). This translocation presumably originated via a centric-break-fusion process that involved chromosomes 1B and 1R as univalents and occurred in breeders' nurseries. The 1RS segment was contributed

by Petkus rye and so far 1B/1R 1B/1R wheat cultivars have no variability for this rye short arm.

There is a prevalent opinion that wheat cultivars with the 1B/1R translocation have a poor bread-baking quality, an opinion that has prompted some breeders to analyze segregates and discard those selections that possess the translocation. Recently (Amaya and Peña pers. commun.), baking on 1B/1R cultivars indicates that poor bread quality is not a universal phenomenon and the quality can be satisfactorily manipulated by bakers. Efforts have been made to reduce the IRS chromosome arm (Koebner and Shepherd 1985, 1986) that employs the *PhPh* mutant as the homoeologous pairing promoter. Other translocations of practical interest are the 5A/5R for copper efficiency and the probable utilization of the 6RL rye arm for cereal cyst nematode resistance.

Induced translocations may be random, partially controlled, or directed. Several random translocations were reported in *Triticale* × wheat crosses (Lukaszewski and Gustafson 1982, 1983) and recently have been phenotypically observed in intergeneric *T. aestivum* × *Agropyron* species hybrid derivatives, thus categorized due to the presence of long, lax spikes, stiff awns, and variable threshability (Mujeeb-Kazi unpubl.). All these *T. aestivum* × *Agropyron* species F₁ hybrids were advanced by top-crossing the F₁ with one or two elite wheat cultivars, thereby exploiting the unreduced egg potential of the F₁. Due to univalency in most of the wheat × *Agropyron* hybrids, there is adequate opportunity for univalent misdivision that to a certain degree could randomly involve wheat and alien chromosomes.

Partially controlled translocations are derived from *T. aestivum* × alien species F₁ hybrids when top-crossed with *T. turgidum*. The derivatives possess 42 chromosomes if the alien species is a diploid, with a meiotic association of 14 bivalents (AABB) + 7 univalents of the D genome + 7 univalents of the alien genome. The 14 univalents set the basis for translocations that are partially controlled. The process can be made more specific by advancing to the alien disomic addition line stage and then top-crossing with *T. turgidum*, in which case a single alien univalent chromosome will have the opportunity to undergo random association via translocation with the seven univalents of the *T. aestivum* D genome.

Direct translocation induction originates through establishing homoeology of the alien disome with wheat chromosome groups; substitution is effected and eventually generated by crosses with euploid *T. aestivum* translocation end-products as a consequence of centric-break-fusion of the two univalents.

Irradiation-induced translocations have been reported in the Triticeae (Sears 1956 for "transfer" involving chromosome 6B; stem-rust resistance from *A. elongatum* to 6A of wheat, Knott 1964; leaf-rust and powdery mildew from rye to 4A of wheat, Driscoll and Jensen 1964; leaf- and stem-rust resistance from *A. elongatum* to 7D of wheat, Sharma and Knott 1986; leaf-, stem- and stripe-rust resistance from *A. intermedium* to 7A of wheat, Weinhuess 1973). The volume of cytological work in detecting translocations is cumbersome and rapid diagnostic procedures will prove beneficial as facilitated by the glucose-phosphate-isomerase nondestructive assay for detecting the 1B/1R translocation in wheat cultivars or segregates.

8 Tissue Culture

Embryo culture in intergeneric hybrids has considerably augmented the divergence of crossability barriers and should continue to extend the range over which wide crosses will be made. It has been the most critical step in the production of primary hexaploid triticale (Bajaj et al. 1978) and presumably will persist as such, in support of the breeders' need to continuously diversify the \times *Triticosecale* (Wittmack) genetic base.

Callus culture based on embryo culture and plant regeneration has been studied with keen interest worldwide. Genetic variation identified cytologically and biochemically in regenerated derivatives has provided a new dimension for breeders to exploit callus-induced variability, with the variable progeny being a consequence of the "somaclonal variation" (Larkin and Scowcroft 1981) phenomenon. Similar variation has recently been observed in several *T. aestivum* and *T. turgidum* cultivars (TCCP 1987). The range of variability in the regenerated plants, however, did not appear to be any different in nature than that possible in mutation breeding approaches using ionizing-, nonionizing irradiation, or chemical mutagenesis where the entire somaclonal variability spectrum appears expressed during M_2 to M_4 generations as is characteristic of macro- and micro-mutational events.

Higher priority for in vitro studies in the Triticeae may relate to in vitro screening for diseases producing toxins and for stress factors. Alien genetic transfers mediated by callus culture promote multiple cytological variations and could also be exploited as an adjunct to *Ph*-mediated F_1 intergeneric hybrid genetic exchanges. The alien exchanges have been demonstrated in wheat \times rye hybrids (Lapitan et al. 1984, 1986, 1988) and are being applied to other intergeneric hybrids (*T. aestivum* \times *Ae. variabilis*) with poor F_1 wheat/alien chromosomal recombination (Ter-Kuile et al. 1987). Amphiploids of intergeneric hybrids represent an important means of germplasm distribution and organized alien genetic component exploitation, particularly for stable amphiploids. It has been rather difficult to induce amphiploidy in several intergeneric hybrids by colchicine treatment, but a recent observation involving regenerated F_1 hybrids of *T. aestivum* \times *Ae. variabilis* and *T. turgidum* \times *Ae. variabilis* demonstrated seed set on an otherwise anticipated self-sterile population (Ter-Kuile et al. 1988). Callus-induced doubling may prove advantageous for combinations otherwise hard to double. A recent review by Lorz et al. (1988) provides more in-depth information on tissue culture and genetic transformation in cereals.

9 Polyhaploid Production

T. aestivum polyhaploids have been produced at over 20 and 40% frequencies in crosses of Chinese Spring wheat with *Zea mays* and *H. bulbosum* (Barclay 1975; Laurie and Bennett 1986). Anther culture-based wheat polyhaploid generation frequencies are significantly lower than the above genetic systems (Inagaki et al.

1987) and beset with aneuploidy. The limitations of germplasm response is also a crucial factor and it may be appropriate to study the response of other highly crossable wheat cultivars like Chinese Spring for attaining further insight into the mechanism. It is crucial to have polyhaploid production extend over a wide array of *T. aestivum* cultivars and other Triticeae germplasm, to make the practical impact necessary to complement a breeders' segregating population, where the instant homozygosity attribute of haploid induction is of value. Polyhaploids of alien species are also essential, since the genomic status in various grasses is still debated, an area that warrants both anther culture and sexual crossing applications.

10 Interspecific Hybridization

In contrast to intergeneric hybridization, interspecific hybrids in the Triticeae are gaining renewed interest primarily due to (1) ease of hybridization (2) genomic similarity of the species with *T. aestivum* and *T. turgidum*, and (3) as a consequence of genomic similarity the potential of en-bloc recessive polygenic transfers. Alien genetic expression is a recognized limitation, but the simplicity of attaining short-term practical returns dominates this constraint. The germplasm (genera, species, and accessions) enables manipulation of the A, B, and D genomes of *T. aestivum* or A, B of *T. turgidum* (Mujeeb-Kazi and Asiedu 1989).

11 Stability of Alien Transfers and Novel Applications

Alien genetic transfers (intergeneric or interspecific) can diversify variability for both biotic and abiotic situations, two aspects that are of considerable functional difference but correlated with genetic stability. In one case a pathogenic system is involved which is vulnerable to mutational events, leading to eventual breakdown of resistance. The other aspect deals with physiological traits devoid of mutational changes and capable of longer stability. Mujeeb-Kazi and Kimber (1985) have referred to these systems as "dynamic" and "static".

Variability originating through alien introgression is additional to conventional breeding efforts and is unique in nature because of genomic diversity or interspecific remoteness. Incorporation of alien genes at the plant level is a time-consuming but rewarding process, and many facets have been clarified over the last decade and a half. Added efficiency to plant level manipulation would be found in novel complementary areas that are anticipated to emerge shortly for monocotyledonous plants, particularly for *Triticum* species. Such breakthroughs will add to plant level genetic manipulation and may also replace several conventional stages. Presumably protoplast fusion and regeneration alone will widen the wide hybridization range by facilitating union of wheat \times alien species that are not yet possible by direct crossing. Transformation has been reported in *Zea mays* (Rhodes et al. 1988); how soon will it be applicable for the Triticeae? We are aware of these futuristic changes, and breeders worldwide are keen to make their programs more efficient. Wide

crosses have already moved into cellular and molecular approaches where the diagnostic techniques are a boon for effecting alien transfers. There are four major groups of markers with applications in wheat wide crosses – morphological, genetic, cytological, and biochemical. Combined use of these markers adds to efficiency. The most useful markers are those that show high levels of polymorphism, are rapid, can be applied to seed endosperm or seedlings, have no deleterious effects, and are inherited in a co-dominant fashion. Application of diagnostic markers would ideally start with the choice of parents for hybridization. One of the considerations should be differences between the parents at several marker loci in order to facilitate screening of derivatives from the cross. The best way to ensure tight linkage between marker loci and those of desirable genes would be to begin with many polymorphic marker loci; a requirement that only RFLP's (restriction fragment length polymorphisms) can provide owing to their multiplicity and high polymorphism. So far the most significant uses of markers in Triticeae and in wheat breeding have been the screening for the glucose phosphate isomerase (GPI) locus in relation to the 1BL/1RS segment translocation; screening for the endopeptidase locus in relation to eyespot resistance; high molecular glutenin subunits in relation to bread-making quality or gliadin patterns in connection with pasta quality. Naturally, applications involving simply inherited traits would be easier, but quantitative trait loci are increasing under marker-assisted studies (Stuber et al. 1987). Moreover, for some characters it is likely to link marker loci to loci for genes of major effect even if the characters are of complex inheritance.

Introgression of alien germplasm into wheat is a research area for which markers constitute almost a *sine qua non*. Fortunately, this is also the area in which markers have the easiest application, owing to the greater genetic distance between species than within species, leading to clearer interspecific differences in DNA sequences and proteins. Applications in this case include aneuploid identification, chromosome assays, hybrid confirmation, and establishment of wheat-alien chromosome homoeologies. The capacity to track the alien chromatin during cytogenetic manipulations would assist in the choice of materials, methods, and population size necessary for an efficient and precise transfer. This characterization of introgressed segments is essential, especially the knowledge of the sizes of the alien segments to assist in making decisions as to what may be required to reduce alien contribution to the minimum necessary for the particular trait in question.

12 Conclusion

Since the reports of Kruse (1967, 1969, 1973, 1974) there has been heightened interest worldwide in the production and exploitation of intergeneric hybrids. Production of hybrids has been simplified, but the need to attain more complex hybrids does exist. The practical goals of a wide crossing program have so far used conventional techniques with subtle incorporation of sophisticated methodology, but in general genetic manipulation in *Triticum* is maintained at the plant level. The enormous array of genetic stocks in *Triticum* offers remarkable opportunities for alien gene transfers and incorporation of homoeologous, introduced segments in

the best location in the recipient wheat chromosomes. This precision will occur by more intensified research that would promote transfers via recombination events and subtle gene transfers; an area of priority in wide cross cytogenetics and breeding. Novel techniques exist or are being developed to complement cytogenetics of alien transfer mechanisms, diversify polyhaploid induction, yield greater precision for callus culture, and establish diagnostic markers to bring efficiency to conventional approaches. It is envisaged that, although the present novel techniques in Triticeae are severely handicapped by lack of suitable vector systems, transformation markers, limited knowledge of gene location and molecular bases of gene expression, a breakthrough should be relatively close. When this happens it will allow a wheat/alien gene transfer program that will cover both conventional protocols and sophisticated novel procedures without any retraction from the relevant cytogenetic and important field application practical goals.

Current and futuristic projections over the next decade indicate no major impediment in wheat-alien crosses to restrict genetic advances at the plant level. The alien introgressed germplasm as a consequence of cytogenetic manipulation forms the backbone of diagnostic technology applications whether these are genome-specific or cover the entire genome. Polygenic alien transfers in intergeneric hybridization are not likely to occur en-bloc, in which case several independent transfers may exist for character selection and combining by breeding through pyramiding of independent genes. Interspecific transfers (presumably less fanciful than intergenerics) need to be integrated into wide crosses. They have a significant advantage when quantitative traits are considered because of the recombining capabilities of these not so alien species with *T. turgidum* or *T. aestivum*, and possess the potential of yielding short-term practical benefits.

The potential for success in wide crosses inevitably resides in linking plant level genetic manipulation with cellular and molecular approaches, with receptivity and cognizance of futuristic changes that after functional refinement should be integrated into current researches for *Triticum* improvement. It should also be recognized that once a transfer is stabilized the necessity remains of ensuring the practical utility of the derived germplasm. This is a gigantic task that requires national and international administrative breeding plus support services to apply the end product from alien genetic transfer programs.

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