The Potential of Wide Hybridization in Wheat Improvement

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ABSTRACT

In their effort to meet the increasing worldwide demand for food, plant breeders are finding less and less appropriate germplasm with desired traits among cultivated crops themselves with which to make needed improvements. Fortunately, useful genetic resources (i. e. important traits for use in crop improvement) are being found among uncultivated plants in the wild. The challenge is to be able to incorporate this "new" germplasm routinely into existing food crops through a technique called wide crossing. Most efforts to transfer alien germplasm from wild plants into cultivated crops have involved the *Triticum* grass species—with the greatest emphasis being placed on improving bread wheat (*T. aestivum* L.). Introgressing alien variability is demarkated into the two distinct areas of long-term intergeneric and short term interspecific hybridization. These essentially are separated on the basis of wheat/alien genomic similarity and level of genetic recombination. Interspecific approach is, thus, favored for genetic introgression. This paper addresses the prevalent state of the wide cross methodology and offers insight into the advances made over the past two decades that make this field promising for crop improvement.

Key words : Wide crosses, triticeae, intergeneric hybridization, interspecific hybridization, alien introgression

INTRODUCTION

Amongst cereals, bread wheat (*Triticum aestivum* $(2n=6x=42=AABBDD)$ is the classical example where wide hybrids involving related genera and species viz., *Aegilops, Agropyron, Secale, Hayraldia, Elymus,* and *Hordeum* have been well investigated. These wild relatives are an important reservoir of useful genes for various traits such as resistance to major diseases, insects, increased tolerance to various soil and environmental stresses and improved nutritional quality. The enormous potential of wide hybridization for wheat improvement is now being realized after several initial barriers have been overcome. Of the 325 species in the triticeae, approximately 250 are perennials (Dewey, 1983). Relatively few of these have been hybridized with wheat, except for the *Thinopyrum* group of species. The status of wide hybridization in wheat has been reviewed (Dewey, 1983; Sharma and Gill, 1983; Mujeeb-Kazi and Kimber, 1985; Mujeeb-Kazi *et al.,* 1989; Asiedu *et al.,* 1989; Laurie *et al.,* 1990; Mujeeb-Kazi, 1993).

Barriers to the production of wide crosses are encountered at various stages in the ontogeny of the hybrid (Mujeeb-Kazi and Kimber, 1985) and are divided into six parts : choice of parents, emasculation procedures, pre-pollination treatment, pollination, post-pollination treatments, and embryo excision and culture. Apart from the practical motivation to introgress genes from the alien species into wheat, intergeneric hybrids offer promise of providing basic cytological, evolutionary or phylogenetic information about the parental species- Whatever the objectives, hybrid production occupies the initial critical step for additional manipulations that permit effective genetic transfers to take place.

From the hybrids produced earlier, successful transfers from a few combinations (wheat/*A. elongatum*, wheat/*A. intermedium*) have been for leaf rust, stem rust, yellow rust, and wheat streak mosaic virus. Various examples of such alien gene transfers have been given in the reviews (Sears, 1981, Sharma and Gill, 1983; Mujeeb-Kazi and Kimber, 1985; Khush and Brar, 1988; Wang, 1989). This paper elucidates wide cross methodology, its techniques and while it identifies certain constraints in the use of alien germplasm for wheat improvement it does highlight the enormous potential of wide crosses in cereal improvement.

PRODUCTION OF HYBRIDS

The production of the earliest intergeneric hybrids was accomplished by application of the simplest techniques of emasculation and pollination similar to those utilized in conventional wheat breeding programs. When more diverse or distant hybridizations were initiated, hybrid production constraints were increased manifold and an array of manipulative techniques emerged. These ranged from pre-pollination to post-pollination hormonal or immunosuppressant influences. Additionally, genotypes, ploidy level, cross direction, and environment all became contributors to hybrid production success. All these aspects have been extensively reported (Sharma and Gill, 1983; Mujeeb-Kazi and Kimber, 1985). A hybrid production procedure in which wheat is the maternal parent is being routinely adopted by us with significant success (Mujeeb-Kazi *et al.*, 1987). The procedure involves bud pollination, a post-pollination gibberellic acid treatment of the maternal tissue for two to four days, embryo excision from 14 to 18 days post-pollination, embryo culture on Murashige and Skoog (1962) or Taira and Larter's (1978) media for small embryos, cold treatment (4°C) to break dormancy and culminating in plantlet differentiation. Alien diploids have been difficult to hybridize with wheat but data (Mujeeb-Kazi, unpublished) seem to indicate that such crossability barriers can be overcome either by reciprocal crosses or by first doubling the alien diploid and using the induced autotetraploid as the pollen parent (Mujeeb *et al*, 1995). Specific examples of intergeneric hybrids produced by this procedure are : *T. aestivum/A. cristatum* (4x), *T. aestivum/Psathyrostachys juncea* (4x), *T. turgidum/Ps. juncea* (4x), in which each hybrid possesses 35, 35 and 28 chromosomes, respectively.

CYTOLOGICAL IDENTIFICATION

Initial hybrid identification is based upon mitotic counts. This technique (Mujeeb-Kazi and Miranda, 1985) appears to be superbly adapted to the range of alien species that exist in the triticeae and merits analyzing its applicability to other taxa. Additional identification can be made by employing chromosome banding techniques. Karyotypic differences have their contribution but positive claim of hybridity must be accompanied by clear meiotic analyses. This permits breeding strategies for each wide hybrid combination to be formulated by the chromosome pairing data analyses, thereby providing a basis for the logical introduction of variation (Kimber, 1984). More recently molecular cytological techniques have augmented diagnostic precision (Rayburn *et al.*, 1993; Islam-Faridi and Mujeeb-Kazi, 1995).

DESCRIPTION OF F1 HYBRIDS

In general, the morphological F1 hybrid plant characteristics are indicative of definite phenotypic differences when compared with the wheat cultivar. Certain hybrids do not express a variable F1 phenotype and irrespective of the cross direction one parent always appears dominant viz., *H. vulgare* and *T. aestivum* or *T. turgidum* where *Triticum* is the dominant parent (Kruse, 1973; Islam *et al.*, 1975; Mujeeb-Kazi and Rodriguez, 1984). An unmodified F1 hybrid phenotype may still possess stuble biochemical component variations, but the ultimate expression of these effects appears somewhat restricted.

Most of the *Triticum* based hybrids have shown an aneuploid chromosome composition (Mujeeb-Kazi *et al.*, 1987). This variation may be restricted to a few chromosomes that are deleted or duplicated, or may even lead to complete genome elimination. A dramatic loss of alien chromosomes was reported by Islam *et al.* (1975, 1981) in wheat/barley F1 hybrids that eventually resulted in a disomic barley chromosome addition. Laurie and Bennett (1986) reported wheat ovules upon fertilization by maize pollen produced haploid wheat embryos following the elimination of maize chromosomes. Recently, haploid wheat plants have been produced from wheat × maize crosses (Laurie and Bennett, 1988; Suenaga and Nakajima, 1989). Though restricted by the presence of recessive *Kr* crossability loci of homoeologous group five chromosomes of wheat, Barclay (1975) earlier obtained a high frequency of wheat polyhaploids in sexual bread wheat/*H. bulbosum* hybrids, an event that Islam *et al.* (1981) considered useful in developing disomic barley chromosome addition lines. Chinese Spring was the *Kr* recessive cultivar in both cases. F1 intergeneric hybrids are usually perennial, can be vegetatively propagated (Mujeeb-Kazi and Bernard, 1985) to give a large population that facilitates the step-wise production of alien chromosome addition lines, derivation of their disomic substitutions using the monosomic procedure or utilizing the

ditelosomics. In intergeneric hybridization, amphiploids form a critical step towards developing normal cytogenetic stocks, but since the amphiploid induction frequency remained alarmingly low (Mujeeb-Kazi *et al.*, 1989) direct production (F1 hybrid × wheat) of backcross I progeny was quite effective and rapid to meet our applied goals. This route does not guarantee normal BC1 progeny for the wheat and alien genomes due to the probability of wheat/wheat, wheat × alien, alien/alien chromosomal translocations, with the latter two events complicating alien addition line production. The translocation aneuploidy, however, augments agricultural applications, that becomes further magnified when aneuploid BC1 progeny is consistently derived from the maternal F1 wheat and alien hybrid source (Mujeeb-Kazi and Bernard, 1982; Mujeeb-Kazi and Rodriguez, 1982, 1983a, b).

Translocations have a significant role in breeding wheats with high yield, stability and wide adaptability (Rajaram *et al.*, 1983) with the promising alien contribution being derived from IRS *Secale cereale* chromosome in the IBL/IRS translocation wheats. The adverse baking quality of IBL/IRS wheats is not so generalized. and rye based translocations carefully engineered may have more impact in the future. Lukaszweski and Gustafson (1982) observed numerous wheat/rye translocations. Koebner and Shepherd (1985) demonstrated a methodology for reducing the IRS segment in IBL/IRS wheats, and the potential of IAL/IRS, 5AS/5RL and 6BS/6RL for greenbug resistance, copper efficiency, and cereal cyst nematode resistance has a demonstrated practical potential. It hence appears that *S. cereale* may have a greater influence on wheat improvement via subtle transfer systems than the other distant species categorized under intergeneric hybridization.

SUBTLE GENETIC TRANSFERS

Centric Break Fusion

Amphiploids, alien chromosome addition, and substitution lines normally introduce more alien genetic variation than is desirable for wheat improvement. Techniques are, therefore. preferred that reduce the alien chromatin to the smallest possible alien introgression without losing the required desirable trait. Spontaneous translocations between wheat and alien chromosomes have been reported (Weinhues, 1973) especially in triticale × wheat crosses (May and Appels, 1982). Most of these are attributed to misdivision of wheat and alien chromosomes in the hemizygous condition and the fusion of non-homologous chromatids. Advantage could be taken of this centric break and fusion capacity of chromosomes by making a monosomic substitution of an alien chromosome with a desired gene (s) for one of its wheat homoeologues and screening its selfed progeny for centric-fusion products. Subject to the affinity between the chromosomes this method could at least reduce the alien chromatin to one chromosome arm.

Irradiation

Alien chromatin may be translocated onto a wheat chromosome by irradiating seeds of a wheat line carrying the critical alien chromosome or by pollinating normal wheat with irradiated pollen from such a wheat-alien chromosome line. Sears (1956) was the first to use ionizing irradiation to induce translocation between non-homologous chromosomes. Using a wheat plant with an isochromosome of *Aegilops umbellulata* ($2n=2x=14$) Sears produced 'Transfer' which has a reciprocal translocation involving wheat chromosome 6B and the isochromosome giving resistance to wheat leaf-rust. Further examples of irradiation-induced translocations are stem-rust resistance from *Agropyron elongatum* ($2n=10x=70$) to chromosome 6A of wheat (Knott, 1964), leaf-rust and powdery mildew resistance from rye (*S. cereale*) to chromosome 4A of wheat (Driscoll and Jensen, 1964), leaf- and stem-rust resistance from *A. elongatum* ($2n=10x=70$) to chromosome 7D of wheat (Sharma and Knott, 1966), and resistance of leaf-, stem-, and yellow rusts from *A. intermedium* to 7A of wheat (Weinhues, 1973).

Although most successful irradiation-induced translocations involve homoeologues (Knott, 1964; Weinhues, 1973), many deleterious exchanges occur. Even when genetic detection of translocations is employed through observation of segregation for the desired trait in progeny of irradiated lines (Sharma and Knott, 1966) confirmation is necessary via cytological observation on F1 hybrids from crossing with euploid wheat. The volume of cytological work required is considered a disadvantage for irradiation induced translocations, and some of the products of such translocations have been associated with depressed yield (Weinhues, 1973; Driscoll, 1981) and poor quality (Sharma and Knott, 1966). Target alien genes near the end of an alien chromosome are more liable to be successfully transferred by translocation.

Induced Recombination

Chromosome pairing in wheat reflects a balance between genes which promote and those which suppress homoeologous pairing (Riley *et al.*, 1973; Fedak and Armstrong, 1981). While pairing promoting factors have been located on chromosomes 3D, 5AL, 5DL, and 5BS, normal pairing in wheat is restricted to homologues by major gene (s) on 5BL (Okamoto, 1957; Riley and Chapman, 1958) and minor genes on 3D, 3A, and 4D (Driscoll, 1972, 1973). Riley *et al.* (1981) have discussed the genetic control of recombination and its manipulations for wheat improvement. Several workers have further demonstrated the formation of multivalents involving homoeologues and synapsis of wheat and alien chromosomes in the absence of the major suppressor of allosyndesis (*Ph1*) on 5BL.

Some genotypes of *Triticum speltoides* (Tausch). Gren. ex Ritcher, *T. longissimum* (Schweinf *et* Muschl.) Bowden and *T. tripsacoides* (Jaub. *et* Spach) Bowden

(=*Aegilops mutica* Boiss.) promote heterogenetic pairing in hybrids with common wheat (Riley and Law, 1965; Riley and Kimber, 1966; Chen and Dvorak, 1984). When an alien species is crossed to a hybrid between wheat and one of the three species is an increase in heterogenetic pairing and recombination. Despite the complication introduced by the probable recombination among chromosomes of all the three species involved, Riley *et al.* (1968) produced the wheat line 'Compair' using the scheme. 'Compair' has stripe rust resistance gene (s) from *Aegilops comosa* on chromosome 2D. Rye also has genes which suppress the activity of the *Phl* gene (Fedak and Armstrong, 1981).

An alien species could be crossed to wheat monosomic 5B or nullisomic 5B tetrasomic 5A/5D. Such progeny would lack the *Phl* and hence have improved chances of wheat-alien recombination. Sears' (1977) mutant line *phlb phlb* may be used in place of mono-5B or nulli-5B tetra 5A/5D and the Fl hybrids either selfed or backcrossed to the mutant line. The choice of material in which allosyndesis is induced is important to the level of precision of the planned recombination and use of the following increasing order of precision has been suggested : wheat-alien hybrids, disomic alien additions, monosomic alien additions, monosomic alien substitutions and monotelosomic alien substitutions. In addition to the *phlb* mutant less effective pairing mutants like *phla* (Wall *et al.*, 1971) and *ph2* (Sears, 1977) are available in hexaploid wheat. Another high-pairing mutation has been obtained through irradiation in cultivar 'Capelli' of *Triticum turgidum* L. em. Morris *et* Sears var *durum* (Giorgi, 1978). Some examples of alien genetic transfer through induced homoeologous recombination are the transfer of leaf- and stem-rust resistance from *A. elongatum* (2n=10x=70) to chromosome 7D of wheat (Sears, 1973) and to chromosome 3D of wheat (Sears, *loc. cit.*). Even wheat-rye chromosome recombination has been obtained in a *phlb phlb* background (Koebner and Shepherd, 1985) despite earlier skepticism (Riley and Kimber, 1966; Law, 1981).

Cell and Tissue Culture

Plant cells and tissues proliferating in culture have been shown to accumulate a lot of genetic variability. Regenerants from callus cultures have been reported to show morphological. cytological, and isozymic variability. While many of the cytological variations are in the form of chromosomal abnormalities like polyploidy, aneuploidy, breakage, and rearrangement, Larkin and Scrowcroft (1981) suggested additional somaclonal variation in the form of gene mutations, etc. They further proposed the possible reduction of homoeologous pairing inhibitions by putting hybrids through a tissue culture cycle. Tissue culture of Fl hybrids, chromosome addition/ substitution lines could promote alien gene introgression (Lapitan *et al.*, 1984, 1888). Larkin *et al.* (1989) emphasized the usefulness of high frequency chromosomal exchanges in wheat cell cultures to introgress alien genes for cereal cyst nematode resistance from rye and barley yellow dwarf resistance from *Thinopyrum*.

Major limitations of the technique are the inability to regenerate plants from cells for many plant species and the difficulty of maintaining the morphogenetic potential of cells over long periods in culture. Moreover, it is not always certain that the characteristic expressed in the cell will also be expressed in the whole organism. The molecular events leading to the observed variability are not well understood. Perhaps, one may question whether the variability pre-exists in the somatic cells of the explant or is solely generated during culture. With the increasing amount of work in this area, other questions like the effects of genotype, age of culture, explant type and also the ratio of epigenetic to truly genetic variability would be answered in addition to removing some of the limitations.

DIAGNOSTIC TOOLS FOR IDENTIFYING ALIEN CHROMATIN

A number of diagnostic tools are essential for keeping track of alien chromosomes during crossing programs and/or for identifying and characterizing the alien segment after a successful transfer. Chromosome size, arm ratio, and satellite status enable recognition of some chromosomes and structural markers like telocentrics and isochromosomes have been used. The variation in plant morphology caused by changed dosage of specific chromosomes and markers based on disease resistance/ susceptibility are also useful. Techniques like Giemsa C- and N-banding have been used for chromosome identification and karyotype analysis in many species in triticeae (Gill and Kimber, 1974; Gerlach, 1977; Gill, 1987). However, even a combination of chromosome morphology and banding patterns are not sufficient for identification of all the various chromosomes in the tribe. Repeatability and consistency of the banding patterns between different laboratories have also been questioned (Van Niekerk and Pienaar, 1983).

Mapped isozyme loci have proved to be valuable markers in genetic and evolutionary studies with wheat and its relatives. Several loci are masked by enzyme structural genes in wheat in addition to biochemical markers for glutenin and gliadin production. Corresponding enzyme marker loci have been identified in other genera/ species of the triticeae (Hart *et al.*, 1980; Hart and Tuleen, 1983; Ainsworth *et al.*, 1984). Most biochemical markers are codominant allowing all possible genotypes to be distinguished in any segregating generation and large numbers of lines can be screened at early stages of plant growth or even by using seed endosperm portions. Recently, molecular markers such as restriction fragment length polymorphism (RFLP) are becoming important in monitoring alien gene introgression. Gale and Sharp (1988) have elaborately reviewed the developments and prospects of isozyme and RFLP markers in wheat improvement.

In situ hybridization is a fast advancing method of chromosome identification. In this method, the distribution of many of the highly repeated sequences is similar to

the C-banding patterns of the specific chromosomes. Restriction of *in situ* hybridi-
zation to special situations was suggested where the staining techniques are ineffective
though easier and cheaper. There are many reports of such cases of the superiority
of *in situ* hybridization where the appropriate probes are available. Examples are
its use in the identification of an *Aegilops sharonensis* chromosome in a wheat
background (Miller *et al.*, 1980); identification of D-genome chromosomes of wheat
(Rayburn and Gill, 1986) and the characterization of a derivative from chromosome
IDS–IRL with a reduced amount of heterochromatin (Koebner *et al*, 1986).
Amplification of repeated DNA sequences has been detected through *in situ*
hybridization in wheat × rye hybrids regenerated from tissue culture (Lapitan *et al.*,
1988). As more probes are developed (Appels *et al.*, 1986) the power of the
technique through the capacity to identify the DNA rather than the product would
become even more evident. More recently both enzymatic (Rayburn *et al.*, 1993)
and fluorescent *in situ* hybridization techniques have been exploited. The latter
(FISH) apparently has gained more usage (Islam Faridi and Mujeeb-Kazi, 1995).

SYNTHETIC GENOME DEVELOPMENT

In alien genetic transfers so far, rather simply inherited traits have been introgressed
(Dewey, 1983) with the *Thinopyrum* group contributing the most. The transfer of
polygenic traits does appear as a major constraint in wide crosses and it is doubtful
that existing techniques can alleviate the expressed constraint by effecting an en-bloc
transfer of all desirable but unmapped genes. Systematic partial transfers, large
population testing, pyramiding independently transferred genes to produce elite
germplasm is apparently the solution that undoubtedly ranks very futuristic.

In the segmental allotetraploids, or partial autopolyploids *(Th. curvifolium, Th.
junceiforme, Th. scirpeum)* or segmental allohexaploids *(Th. junceum)*, or segmental
autoallohexaploids *(Th. intermedium-varnense)* there is the possibility of exploiting
events of the BCIFI generation that would make germplasm available with synthetic
genomes. The direct merit of synthetic genomes or amphiploids emanates from
their direct cultivation in production areas of constraints for wheat. The
amphiploid would have to possess reasonable qualities to warrant such an approach.
It has been expressed (Dr. Colin Law, P. B l., Cambridge, pers. comm. with A. M-
K) that the *T. aestivum/Th. bessarabicum* amphiploid $(2n=8x=56)$ may be ideal as
a crop in the saline areas where wheat production is prohibited. The blue aleurone
tinge in the amphiploid and the rust susceptible wheat cultivar involved may require
some improvement attention. The amphiploid crop concept, however, is worth
exploring, even for other complex traits for which variability and cultivation is
severely restricted in the conventional wheat germplasm.

Some breeding methodology inputs may assist in improving the synthetic genome
derivatives where the Fl (wheat/alien) is crossed with another elite wheat cultivar,

and selections are practised at subsequent selfings of the resultant BCI selfed derivatives i. e. Variety 1/Alien 4x species/Variety 2=BCIF n (selfed and selected).

In autoallohexaploids, the process would be : Variety 1/Alien 6x/Variety 2=BCI (AABBDDEIE2Z)→ BCIF n (selfed and selected). The selfed derivatives will form partial synthetics genomically represented as AABBDDE, m E2 m (where m is For E1 and E2 genomic modifications). The resulting wheat varietal improvement will be a consequence of varietal recombination and segregation that will be at a decided practical advantage over the single wheat cultivar present in the amphiploid combination.

STABILITY OF ALIEN GENETIC TRANSFERS

The introduction of alien variation may involve loci for disease reaction or for physiological traits. Undoubtedly, it may be inferred that perennial alien species would have durable resistance capacities because of their habitat, but we consider aspects pertaining to disease reactions as mutable and consequently resistances fall into a ' dynamic' category; hence, if the pathogen mutates the resistance breaks down. This is equivalent to any 'dynamic' system common to the conventional systems. Physiological traits, however, are free of the above restriction and alien transfers for such traits will be longer lasting or considered as 'static' (Mujeeb-Kazi and Kimber, 1985).

Wide cross programs are generally not designed towards varietal release. The programs are structured at incorporating novel gene sources for the breeders, thereby enhancing their arsenal of already available genetic variability, that if biotic is categorized as 'dynamic' and is vulnerable. Hence, the more diverse the genetic base, the higher the crop stability insurance. In certain situations, existing variability for breeding purposes is negligible and resort must be made to diverse sources. With wide crosses being futuristic and gene transfers complicated to achieve, short-term productivity goals need to be kept in balance. The short-term alien gene transfers result from recombination derived events where interspecific crosses are a priority (Mujeeb-Kazi, 1992, 1993). This is supported by the fact that the majority of the alien variation introductions in the triticeae have been accomplished by recombination, and for maximum benefit the smallest piece of alien genetic material is a necessity since it will control the desired phenotype and not alter the other essential attributes of the recipient species. Consequently, in the triticeae where extensive cytogenetic understanding is prevalent and genetic stocks reside, the newer novel techniques may have serious limitations. Induced recombination techniques will potentially place introduced segments ideally from the alien species into the wheat genome and continue to rank extremely high as the preferred method of crop improvement.

We should be cognizant of the fact that simply inherited traits are at a decided advantage and such transfers have indeed been accomplished. Presumably with the

numerous new intergeneric hybrids now available in our program, more emphasis should be devoted towards study of the previously known simply controlled traits. This would provide new variation under short term conditions for applied wheat breeding goals. The quantitative traits would remain long term and will require better understanding. It is doubtful whether the genomic status of the alien species (Dewey, 1983) will prove readily beneficial towards effecting multiple beneficial alien transfers primarily because of the reduced frequency of Fl, recombinational events in a vast majority of the hybrids produced. It is plausible to advocate the superior promise of attaining practical agricultural benefits in a relatively short term from the A, B and D genome donor accessions to hexaploid wheat as well as durums.

Genome extractions (AABB) from *T. aestivum* and resynthesis (AABBDD) utilizing the D genomes of pest resistant *T. tauschii* alien accessions may be a extremely stronger genetic tool for quantitative traits. Direct D genome transfers to bread wheat are another viable option (Mujeeb-Kazi. 1992). This, however, should not discount the intergenomic suppression phenomenon that could render the resistant alien accessions relatively ineffective despite the manipulation because of modifying interactive factors on the A and B genomes.

CONCLUSION

Ever since the reports of intergeneric hybridization in cereals by Kruse (1967. 1973) there has been heightened interest in this area world wide. The development has undergone the distinct phases of hybrid production, their academic value, and the ultimate practical agricultural gain attention. Hybrid production techniques have been simplified and we can conclude that hybrids earlier found difficult to produce can now be attained with considerable ease (Mujeeb-Kazi *et al.*, 1995). The advantages of the *PhPh* genetic systems in the mutant backgrounds have yet to be significantly used. The 5B genetic system offers promise but has not been that simplistic to exploit. The superior crossability of *T. aestivum* cv. Chinese Spring has been advantageous in hybrid production, but an obstacle, when early generation derivatives are field tested. Integrating top crossing methodologies have improved progeny acceptability, but lead to a confounding of results as a consequence of transgressive segregation that emerges due to presence of the different wheats involved in crossing Applied usage of two other highly crossable cultivars (Asakazekomugi and Fukohokomugi) has yet to be exploited. Aneuploidy in Fl hybrids and their backcross I derivatives have decidedly more systematic cytological disadvantages than merits, but for applied breeding approach this variability is a boon with superb potential. Amphiploid production frequency has been quite low and needs more attention. The taxonomic and nomenclatural changes proposed for range grasses (Dewey, 1983) have elucidated more of the genome relationship and do facilitate additional development of fertile backcross I derivatives with complete

or partial synthetic genomes. Despite this 'new crop' potential of amphiploids and fertile backcross I derivatives we feel that recombinational events and subtle gene transfers would be the priority for wheat improvement primarily because of the known genetic potential of targeted homoeologous introgression that abound for *Triticum* and the relative case that exists for enforcing such genetic manipulation strategies. Novel techniques are definitely going to have their place, but it remains doubtful whether such techniques will have the capability to introduce into wheat desired alien genetic material so as to integrate appropriately with the wheat genomes. These techniques are handicapped by the lack of suitable genetic vectors and transformation systems together with the limited knowledge of gene locations for many important plant characteristics and of the molecular bases of gene expression. Presumably, technique usage as diagnostic tools would be the initial stage in assisting wheat improvement programs.

Alien species may have been overly accredited as sources for wheat improvement, discounting the consideration that must be made for the genetics of the trait and the genetics of the controlling character in the alien species. It has become obvious to us through our research that improvement for simply inherited traits would be swifter than for the complex polygenic traits, which can be handled only on a long-term basis. This mode of improvement would stand common to all approaches, and it is difficult to envision any short-cuts for complex transfers unless the methodology is dramatically changed. It is here that the interspecific breeding approach has the short-term complex character handling advantage.

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