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# 3.2

# Interspecific and intergeneric hybridization in the Triticeae for wheat improvement

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In all situations the early generations derived from hybridizations between wheat and alien species tend to be poor agronomic plant types. However, by using appropriate breeding methodologies plant types can be significantly improved phenotypically up to the state where alien disomic chromosome additions or derivatives with subtle alien introgression are produced (Mujeeb-Kazi and Asiedu, 1989). Through the application of such methodologies, advanced progenies with disease resistance can be obtained; indeed, such progrenies have resulted from combinations of *Triticum aestivum/Agropyron curvifolium (Thinopyrum curvifolium)* (Villareal et al., 1992a). The derivatives offer resistance to *Helminthosporium sativum* and have initially also demonstrated a resistant response to *Fusarium graminearum* and *Septoria* species. Although the specifics of the alien transfer are yet to be elucidated, from our work at the International Maize and Wheat Improvement Center (CIMMYT) we believe that events similar to that elaborated for low-pairing $F_1$ hybrids (Mujeeb-Kazi et al., 1987) are possible. Additional species contributing towards biotic/abiotic stress resistance that we are exploiting are *Th. bessarabicum, Th. distichum* and *Th. elongatum*. All of the above wheat/alien combinations fall into the intergeneric hybridization category. In this chapter, systematic transfers, with the emphasis on salinity, polyhaploidy and *ph*-induced genetic manipulation, are elaborated upon.

## INTERGENERIC HYBRIDIZATION

The annual/perennial members of the tribe Triticeae provide tremendous genetic variability (Dewey, 1984; Mujeeb-Kazi and Kimber, 1985). In contrast to interspecific hybridization, these species are genomically quite diverse and rather difficult to hybridize with wheat; where successfully combined, the hybrids exhibit little or no allosyndetic meiotic association. Thus, beneficial alien transfers are inevitably time consuming. Despite these limitations, significant advances have been made over the past two decades (Kruse, 1973; Islam et al., 1981; Sharma and Gill, 1983; Mujeeb-Kazi and Kimber, 1985; Mujeeb-Kazi et al., 1987, 1989; Gill, 1989; Mujeeb-Kazi and Asiedu, 1989, 1990). The evolution, since the pioneering hybridization results of Kruse (1967, 1969, 1973), has been in the

exploitation of the *ph* or *ph* locus on the long arm of chromosome 5B, a locus that regulates pairing associations in euploid wheat. When its varied genetic stocks are utilized and hybridized with otherwise low-pairing alien species, the resultant $F_1$ hybrids have a desirable modification of chromosomal associations at metaphase I. An example of this is the *T. aestivum* x *Th. bessarabicum* $F_1$ hybrid; the hybrid has been produced by Alonso and Kimber (1980), Mujeeb-Kazi (1982), Sharma and Gill (1983), Forster and Miller (1985) and Mujeeb-Kazi et al. (1987). In all cases, the alien species was hybridized with the *T. aestivum* cv. Chinese Spring, yielding a metaphase I chromosomal association of less than or closer to 1 bivalent per cell in the 28 chromosome hybrids (*see* Table 1). By hybridizing *Th. bessarabicum* with a monosomic 5B stock of Chinese Spring (Forster and Miller, 1985), substantially higher meiotic pairing was observed (*see* Table 1) but advanced derivatives from these high-pairing 27 chromosome hybrids lacking chromosome 5B were not obtained. Another mechanism of inducing recombination appeared feasible through the use of the *ph1b* system prevalent in Chinese Spring (Sears, 1977).

**Table 1 Meiotic chromosomal pairing association in hybrids of *Thinopyrum bessarabicum* (2n = 2x = 14; JJ) with genetic stocks of *Triticum aestivum* L. cv. Chinese Spring (CS) as the female parent**

| Female parent | Metaphase I chromosomal associations | | | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|
| | I | II Ring | II Rod | III | IV | V | VI | VII | |
| CS | 27.60 | | 0.02 | | | | | | Alonso and Kimber (1980) |
| CS | 24.80 | 0.08 | 1.51 | 0.02 | | | | | Mujeeb-Kazi (1982) |
| CS | 26.23 | 0.04 | 0.83 | 0.01 | | | | | Sharma and Gill (1983) |
| CS | 27.67 | 0.03 | 0.13 | | | | | | Forster and Miller (1985) |
| CS m-5B (i) | 8.46 | 1.71 | 2.39 | 2.54 | 0.58 | 0.07 | | | Forster and Miller (1985) |
| CS m-5B (ii) | 11.07 | 2.18 | 2.68 | 1.36 | 0.18 | | 0.07 | 0.04 | |
| CS *ph1b* | 7.80 | 4.05 | 3.9 | 0.7 | 0.20 | 0.03 | 0.10 | | Mujeeb-Kazi et al. (1988) |

The system was exploited by Sharma and Gill (1986), who produced several $F_1$ hybrids between *Aegilops* species with Chinese Spring *ph1b* as a female parent. Cytogenetic analysis of the hybrid revealed enhanced meiotic associations at metaphase I compared to the relative check hybrids of the alien species with Chinese Spring *Ph Ph*. Unfortunately, however, none of these high-pairing $F_1$ hybrids could be exploited because neither amphiploids nor $BC_1$ derivatives could be obtained (presumably, an influence of the *ph1b* genetic stocks maintenance). Subsequently, Mujeeb-Kazi et al. (1988) produced an $F_1$ combination between *T. aestivum ph1b* x *Th. bessarabicum* that exhibited high pairing (*see* Table 1). This could not be advanced by back-crossing with *ph1b* but a $BC_1$ was obtained by pollinating the $F_1$ hybrid with Chinese Spring (*ph ph*). This allows the $BC_1$ derivative to be heterozygous for the *ph* locus (*Ph ph*) which, upon crossing with maize, should yield haploids that segregate for the *ph* and *ph* locus and high-pairing derivatives could be selected; this proposition has yet to be tested (Mujeeb-Kazi et al., 1992a). There is a good possibility of detecting transfers from *Th. bessarabicum* using the above *ph1b* exchange system as, through addition line and biochemical studies, several markers have been established. The various markers complement each other, ranging

from cytological (C-banding positive) and morphological to a group of biochemical identifiers for all seven homoeologous groups (*see* Table 2). For development of the above classifiers, disomic additions have facilitated interpretations, their stability greatly contributing to repeated confirmation and subsequent tracking in substitution line development. The stability of the disomic additions is expressed as 22 bivalents at metaphase I, a normal 22 + 22 split at anaphase I culminating in adequate self-fertile progeny for the respective disomic line.

**Table 2** **Some diagnostic markers that have assisted in the development of *Thinopyrum bessarabicum* (2n = 2x = 14, JJ) addition lines in *Triticum aestivum* L. 2n = 6x = 42, AABBDD)**

| Homoeologous group | Morphological marker | Biochemical marker |
|---|---|---|
| 1 | x | MDH |
| 2 | Slender spike | SOD |
| 3 | Solid stem | EST |
| 4 | Blue aleurone | PGM |
| 5 | Clavate spike | β-AMY |
| 6 | x | GOT |
| 7 | x | α–AMY |

For attributes such as the salinity tolerance that characterizes *Th. bessarabicum*, our initial screening (Mujeeb-Kazi et al., 1992a) suggests that more than one alien chromosome is involved (*see* Table 3) for the salinity characters. The elevated dry weight and K:Na discrimination values are the diagnostics. It appears that for such a situation the early *ph* manipulation subsequently mediated by polyhaploidy and multiple disomy will prove advantageous.

**Table 3** **Salinity hydroculture screening of some promising wheat/*Thinopyrum bessarabicum* disomic addition lines with 44 chromosomes at 150 mol/m³ NaCl measured after 50 days of full stress[a]**

| Amphiploid and addition lines | Chromosome number | Dry weight (g) | K/Na |
|---|---|---|---|
| Chinese Spring | 42 | 4.5 | 4.5 |
| Chinese Spring/*Th. bessarabicum* | 56 | 3.7 | 9.2 |
| + 3J | 44 | 1.0 | 7.9 |
| + 3J/7J | 44 | 2.7 | 4.3 |
| + 7J | 44 | 1.4 | 7.2 |
| Yecora | 42 | 1.1 | 3.7 |

Note: a Data tabulated for dry weight (g) and Na plus K from plant sap.

## INTERSPECIFIC HYBRIDIZATION

The improvement of bread wheat (*T. aestivum* L.; 2n = 6x = 42; AABBDD) using conventional procedures has essentially exploited intervarietal hybridization processes. These are some constraints to crossing in these processes and invariably all associations of parental traits and segregation are based upon genetic recombination. Thus, if a varied genepool is to be tapped, high priority in effecting alien transfers should be given to utilizing the innumerable alien accessions possessing reasonable proximity to the A, B or D genomes because of genomic similarity, ease of hybridization and the ensuing high frequency of enhanced recombination. This implies that wheat improvement can be targeted for any of the three genomes, A, B or D.

Several accessions of the diploid source are available. Among the potential candidates are *T. urartu, T. monococcum* or *T. boeoticum* for the A genome, *Aegilops speltoides* as a *Sitopsis* section diploid for allowing recombinational transfers into the B genome, and *T. tauschii (Ae. squarrosa)* for wheat improvement via the D genome. A useful reference on other promising sources is Kimber and Feldman (1987). The procedures of incorporating alien variability differ among researchers, as does the choice of the genomic source. As a starting point, we have concentrated on exploiting the D genome accessions of *T. tauschii (Ae. squarrosa)* in a variety of ways, outlined below:

- Hybridization of *T. turgidum* (2n = 4x = 28, AABB) cultivars (resistant or susceptible for a particular attribute) with *T. tauschii* resistant accessions (2n = 2x = 14, DD), doubling the 21 chromosome $F_1$ hybrids (induced or spontaneous) to yield the 42 chromosome synthetic hexaploids (2n = 6x = 42, AABBDD); the synthetic hexaploids, if found after appropriate stress screening to be resistant or tolerant, are used in resistance transfers to other *T. aestivum* cultivars by conventional crossing methods.

- Hybridization of elite *T. aestivum* cultivars with appropriate *T. tauschii* accessions, and back-crossing the ABDD $F_1$ hybrid with the same elite *T. aestivum* cultivar as used in the initial cross in order to rapidly provide improved $BC_1$ derivatives with AABBDD genomes, five genomes (AABBD) of which resemble the elite wheat cultivar used in the cross.

- Extracting the AABB genomes from commercial *T. aestivum* cultivars and then developing hexaploids by crossing with desired *T. tauschii* accessions; the procedure allows very stringent analysis of the genetic contribution of the alien D genome, with negligible interference from the A and B genome recombinational segregation that is rampant in the first two procedures.

It is imperative that the resistance of the D genome from *T. tauschii* be identified because genetic factors on the A and B genomes may mask or modify its expression. This, however, is not a universal phenomenon. The observations of Multani et al. (1988) indicate that the Karnal bunt disease resistance characters of *T. tauschii* were expressed in synthetic hexaploids where the *T. turgidum* base cultivar was susceptible. A similar picture exists for *H. sativum, Fusarium* and salt (Mujeeb-Kazi et al., 1992b).

## SOME PRACTICAL CONSIDERATIONS

There are two essential requirements for the efficient exploitation of *T. tauschii* variability: reliable screening for biotic and abiotic factors; and hybridization with *Triticum* species. Most researchers give priority to direct *T. tauschii* hybridization with *T. aestivum* cultivars because back-crosses into $F_1$

hybrids readily give 11/12ths (or 92%) of the genotype of the recurrent parent in one growing season (Alonso and Kimber, 1984; Gill and Raupp, 1987; Cox et al., 1990). The conclusion reached by Alonso and Kimber (1984) was based on their work on stem rust transfers from *T. tauschii* into Chinese Spring.

When screening constraints for *T. tauschii* accessions occur, an acceptable solution is to sacrifice efficiency for practicality. Such constraints exist in reliably identifying the resistance or tolerance of *T. tauschii* accessions to *H. sativum, F. graminearum* and salinity. However, the crosses between *T. turgidum* cultivars and *T. tauschii* accessions, leading to synthetic hexaploids, do not have this problem and give conclusive resistance screening data.

Screening at the hexaploid level for *Helminthosporium, Fusarium* and salt is viable because the *T. turgidum* cultivars are susceptible. Screening synthetic hexaploids, without prior knowledge of the resistance/tolerance of *T. tauschii* accessions because of the extensive diversity present in *T. tauschii*, has yielded selections that have positive value for wheat improvement. The intricacies of the A, B and D genome associations that exist are circumvented and even if the resistance/tolerance effect observed is diluted in the hexaploid being screened, it possesses a level recognizably higher than that demonstrated by our wheat germplasm for *H. sativum, F. graminearum* and salinity. We are not discounting the fact that D genome interaction with the A and B genomes of durum wheat does exist through gene suppression or enhancement mechanisms, with the former being prevalent, as shown by the dilution effects of the resistant *T. tauschii* rust genes at the synthetic hexaploid level (Dyck and Kerber, 1970; Kerber and Dyck, 1978). However, a word of caution is needed here as such generalizations tend to become accepted fact, thus establishing stringent criteria from which any departure appears controversial but which we see as logical in our hexaploid screening. In our seedling leaf rust studies using synthetic hexaploids (Villareal et al., 1992b) a leaf rust-resistant *T. turgidum* cultivar (Altar 84) was hybridized with two seedling leaf rust-susceptible *T. tauschii* accessions (221 and 223). In the two derived synthetic hexaploids, seedling resistance was expressed for the 221 combination but not for the 223 combination, again illustrating that generalizations may not be valid for all synthetic hexaploids. Now, with the wide array of genetic diversity that we have generated, further elucidation of the D genome interactions with the A and B genomes will inevitably emerge and will presumably be more explicit for simply inherited characters.

As resistant/tolerant synthetic hexaploids have been identified, the following options are available for exploiting the germplasm for wheat improvement:

- Exploit the hexaploids by crosses with susceptible *T. aestivum* cultivars and select the resistant/tolerant segregants, exercising initial caution regarding the necrosis genes present in the synthetics as a consequence of the *T. turgidum* cultivars

- From the resistant/tolerant synthetic hexaploids, exploit the *T. tauschii* accessions by direct crosses with the elite but susceptible *T. aestivum* cultivars, using recurrent back-crossing with *T. aestivum* parents, coupled with cytology to extract stable 2n = 6x = 42 euploids.

Using this information we have now targeted *T. tauschii* accessions for direct hybridization with susceptible and elite *T. aestivum* cultivars: Ciano 79 and Bacanora for *H. sativum*, Seri 82 and Opata for *F. graminearum*, and Oasis for salt tolerance. The crossing success demonstrated by Alonso and Kimber (1984) with Chinese Spring has been obtained with all of these elite cultivars. However, there are several options available for achieving even higher crossing success (Gill and Raupp, 1987; Riera-Lizarazu and Mujeeb-Kazi, 1990), particularly for the reciprocal cross (*T. tauschii* x *T. aestivum*) where the minute embryo size and poor plantlet regeneration appear to be the main limitations.

In those situations where the screening of *T. tauschii* accessions was conclusive (for example, *Neovossia indica* or Karnal bunt), the resistant accessions have been directly hybridized with the susceptible *T. aestivum* cv. Seri 82 and *T. aestivum* cv. Bacanora. Reciprocal crosses were also made, and from the 247 $F_1$ hybrids obtained nearly all of them had the expected $2n = 4x = 28$, ABDD constitution. Only three hybrids had 27 chromosomes. Two back-crosses and selfings should open the way to the euploid 42 chromosome plant status and their eventual screening for resistance.

The D genome RFLP linkage map is being quite extensively developed in molecular laboratories; the highly polymorphic synthetic hexaploids, as a consequence of *T. tauschii*, will make a positive contribution to this. So far, in research being conducted by CIMMYT in collaboration with Cornell University, USA, some *T. aestivum* cultivars and synthetic hexaploids have been identified as being highly polymorphic. $F_1$ progeny from their crosses have been produced and double haploids developed. Other synthetics with positive agricultural attributes could be subjected to molecular analysis. New synthetics covering more *T. tauschii* accessions than our present 250 are also being produced, with the emphasis subsequently being placed on achieving direct transfers from *T. tauschii*-targeted accessions to *T. aestivum*. These approaches should contribute to the availability of additional genetic variability for wheat breeding utilization, germplasm conservation and global distribution.

## Discussion

*M. Baum:* Are you not concerned about the residual background of Chinese Spring in your interspecific hybrids using the *ph* mutant and how would you evaluate the chances of using irradiation or immature inflorescence culture to induce gene transfer?

*A. Mujeeb-Kazi:* To answer your first question, the Chinese Spring effects can be eliminated by top-crossing with elite *Triticum aestivum* cultivars as shown by the work on material resistant to *Helminthosporium sativum*. Molecular analyses, carried out by CIMMYT in collaboration with Cornell University, did not detect any traces of Chinese Spring segments in the *Thinopyrum curvifolium* derivatives. So, by making two back-crosses to commercial cultivars you can lose Chinese Spring effects completely.

In answer to your second question, the paper presented at this workshop by Dr Kimber identified some models of the usages of irradiation. Although theoretically the procedure is very sound, and there are several examples in the literature, I would like to see it commercially exploited; to me it seems that it has limited practical use. The IA/IR translocation germplasm (from the late E. Sebesta) seems to be the only recognized example of practical application.

As to your third point, I would personally place very low priority on 'culture' for gene transfer. Genetic manipulation procedures are more systematic and preferable within the Triticeae.

*H.S. Dhaliwal: Triticum durum* possesses very poor K/Na discriminating factor when compared to bread wheats. Durum wheats are much more susceptible to salinity than bread wheats. Dr Wyn Jones's work at Bangor, UK has shown considerable variability for the K/Na discriminating system existing in *T. boeoticum*, *T. urartu* and *T. dicoccoides*. These species should be exploited through crosses to improve tolerance in durum wheats.

*A. Mujeeb-Kazi:* Your comment is very valid. At CIMMYT the emphasis has been on bread wheats. But recently the A genome species have been hybridized with *T. turgidum* cultivars in an attempt to expoit A genome exchange. This should, however, not discount the possible exchanges between the A and D genome for durum improvement via the Cappelli *ph* mutant.

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