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The Production, Cytology and Practicality of Wide Hybrids in the *Triticeae*.

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Abstract

Wide hybrids are both theoretically interesting and often of practical value. There have been significant advances in the production, analysis and utilization of wide hybrids in the *Triticeae*. These advances are described, partly as documentation of the progress that has been made and partly as the basis for further developments.

The practical motivation to make wide hybrids is, in many cases, the desire to introduce very desirable characteristics from the related, alien species into the cultivated forms. Further motivation arises from the possibility of acquisition of basic cytological, evolutionary or phylogenetic information about the parental species involved in the hybrid. It is not surprising, therefore, that wide hybrids in the *Triticeae* have been both attempted and studied for some considerable time.

It is now over 100 years since the first wide hybrid was consciously made in the *Triticeae*, and this was between wheat and rye (Wilson 1876). Rimpau (1891) described 12 plants that he recovered from seed on a presumably doubled sector in a wheat-rye hybrid, and this must represent the first Triticale. Similar very early studies of wheat-barley hybridization were made by Farrer (1904) and others; however, Shepherd and Islam (1981) conclude that it is improbable that any true hybrids were obtained.

Many hybrids involving *Triticum* and species of the former genus *Aegilops* were made during the 1920's and 1930's (see Kihara 1937, for example), from which the genomic relationships of the genus were derived (see Lilienfeld 1951). However, the large scale practical use of the hybrids was delayed until the advent of colchicine (Eigsti and Dustin 1955, for review) in the late 1930's. The ability to double the chromosome number of hybrids had both practical and theoretical consequences. The production of fertile amphiploids allowed the considerable development of Triticale as an emerging crop (Gupta and Priyadarshan 1982) and also advanced the evolutionary studies in the group when McFadden and Sears (1946) both resynthesised *T. aestivum* and thereby recognized the donor of

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the D genome.

The major remaining problems limiting the use of wide hybrids are now the barriers of crossability and embryo development. As soon as any progress is made in lowering these barriers, then the range of wide hybrids that are possible generally increases, and the lowering of the barriers also causes workers to examine the possibilities of yet even wider hybrids. Recognizing that difficulties associated with hybridization and embryo development will always be present, it is possible to record advances in techniques allowing previously impossible hybrids to be recovered.

This paper describes the practical methodology currently available for the production of wide hybrids in the **Triticeae**, the analysis of their cytology, and the selection of techniques for the introduction of desirable variation from the hybrid (or its amphiploid).

PRODUCTION

The production of the earliest interspecific and intergeneric hybrids was accomplished by the aid of the simplest techniques of emasculation and pollination that were in conventional use in wheat-breeding programs. By these techniques many important hybrids were and still are made. The extensive series of crosses made by Kihara, his colleagues and others can be cited as examples (See table page 12, Wheat Information Service, vol 1, 1954 by Anonymous). A more recent tabulation of hybrids involving wheat and its relatives is maintained by Kimber (see Kimber and Abu Bakar, 1979) and currently contains information on some 1104 hybrids and 270 bibliographic references.

In the production of this large range of hybrids considerable variation in the difficulty of making particular hybrids was observed. Some, **T. aestivum** x **T. turgidum** or **T. aestivum** x **T. cylindricum** for example, are quite easy to make; while others, **T. aestivum** x **T. tauschii** or **H. vulgare** x **T. aestivum**, for example, are much more difficult. The first hybrid of **T. aestivum** x **T. tauschii** was sought and attempted by many workers (personal communications) and was actually made by conventional emasculation and pollination techniques, but only one seed was recovered (Riley and Chapman, 1960). Regular production of hybrids between **Hordeum** and **Triticum**, which may have been made as early as 1904 by Farrer, had to await the recognition by Kruse (1973) that embryos could be rescued by applying gibberellic acid to the developing ovule and subsequently culturing the embryo on an artificial medium. The development by Kruse of this type of technique not only allowed the production of that particular intergeneric hybrid but stimulated renewed interest in the whole field of wide hybridization.

Barriers to the production of wide crosses are found at various stages in the ontogeny of the hybrid. For the purposes of this contribution they will be divided into six parts: first, choice of parents; second, emasculation procedures; third, pre-pollination treatments; fourth, pollination; fifth, post-pollination treatments; and sixth, embryo rescue and culture.

Since it is possible that most of the easy hybrid combinations have been made, it is obvious that the choice of parent and the direction of the cross becomes more important in subsequent work. The low frequency of the production of viable embryos in some hybrid combinations must indicate that it is essential to place together pollen and ovules that are genetically compatible. At the present time it would appear that there is little possibility of selecting parents prior to making the cross, for the only way to determine compatibility is to make a cross. Therefore, if difficulty is being experienced in making a particular hybrid combination, the only practical solution is to increase the range of parental genotypes involved and to attempt to make the reciprocal combination.

Brink and Cooper (1940) described and discussed the effects of particular genotypes, ploidy level and the choice of which species was the female parent in interspecific hybridization. In general it has been the practice, at least in the wheat group of species, to use the species with the higher ploidy as the female parent. There are at least two reasons for this practice: First, there would appear to be less imbalance between the chromosome numbers of the embryo and endosperm, and second, it is generally easier to emasculate the hexaploid **T. aestivum** than the tightly invested florets of the related alien species. However, the early production of wheat-barley hybrids was accomplished with the lower-chromosome-number barley as the female, and Zhao and Kimber (1984) record the hybrid **T. tauschii** x **T. aestivum**. Similarly, Sharma and Gill (1983) made hybrids between **Agropyron ciliare** and **A. yezoense** and **T. aestivum**; and the hybrids **A. trachycaulum** x **T. aestivum** (Mujeeb-Kazi, 1980), **A. fibrosum** x **T. aestivum** (Mujeeb-Kazi and Bernard, 1982) and **Elymus canadensis** x **T. aestivum** (Mujeeb-Kazi and Bernard, 1983) all had the lower-chromosome-number parent as the female. So it would appear that other hybrids which have not been possible may be recovered if the reciprocal combination is attempted.

Emasculation procedures can also affect the production of hybrids. The extensive production of hybrids in the CIMMYT program (see CIMMYT Annual Report, 1981 and 1982) has all been accomplished following clipping the tops of the glumes of the female parent and extracting the anthers with forceps. Other workers (personal communications) prefer not to clip the tops of the glumes. It would seem that at very high temperatures there may be some advantage in not clipping, as this will reduce the chance of drying the stigma. Drying may be a major problem in some of the wild species. It is almost always advantageous to remove awns.

The development of cytoplasmic male sterility in *T. aestivum* has allowed the possibility of making hybrids without the mechanical emasculation of the female parent. However, consideration must be given to the possibility that the system producing the male sterility may also cause sterility in the hybrid or its derivatives. Metzger (personal communication) has induced male sterility in many species by cold treatment of the developing spike prior to microsporogenesis, and this may be a new practical tool to aid wide hybridization. The availability of chemicals that will induce male sterility without affecting ovule or embryo development will greatly enhance the technology of hybrid production.

Pre-pollination chemical treatments have been used by various workers with varying success. In general it was considered that these treatments influenced pollen-tube growth, gynoecium longevity, micropylar barriers and the delivery of the male gametes through the pollen tube. Treatments with immuno-suppressants (Bates, Mujeeb and Waters, 1976), 2-4, di-chloro-phenoxy-acetic acid (Kruse, 1974) and gibberellic acid (Larter and Chaubey, 1965) have been reported, but except for gibberellic acid they do not seem to have come into widespread usage.

Characteristically the stigmas of this group of species indicate a receptiveness for pollination by a rapid elongation of cells producing a fluffy appearance. In addition the glumes of some of the species (*T. speltoides* and *T. tripsacoides* for example) tend to gape at this time or slightly later. Pollination is usually made at this time; however Mujeeb-Kazi, Roldan and Miranda (1984) made previously unattainable hybrids by pollinating before the stigma gave indications of receptiveness. It would seem that this early pollination circumvents barriers to fertilization that develop as the stigma matures (Stich, 1984). In addition, Kruse (personal communication) found that first pollination with pollen inactivated either with heat or UV radiation followed by normal pollen caused an increase in the frequency of recovery of hybrids of *T. aestivum* x *H. vulgare*.

Kruse (1973) demonstrated the significance of post-pollination treatment consisting of one application of a 75ppm solution of gibberellic acid (GA3) to the stigma and ovule wall in the assistance of the developing embryo. Though up to 10 daily post-pollination applications have been tried, the authors use a single application of a solution of 75ppm of GA3; it would appear that this treatment is equally effective, and at the same time the single application reduces the risk of accidental out-pollination and decreases the labor involved.

Embryo excision and culture on artificial media is the development that has enhanced the production and utilization of wide hybrids more than any other technique. Various media have been employed but those which seem to be in common usage were developed by Murashige and Skoog (1962) and Taira and Larter (1978).

Embryo rescue and culture is aimed at removing the embryo, aseptically, as late as possible in its development yet still early enough to allow its continued development on artificial medium. Endosperm degeneration may start earlier and seems to be closely related to the cessation of growth of the embryo. Characteristically in wide hybrids embryo development tends to slow down about eight days after pollination, and in 10 to 14 days the embryo often ceases development altogether. Embryos of the hybrid *Hordeum vulgare* x *Secale cereale* (Fedak, 1977) were rescued and successfully cultured only 12 to 14 days after pollination; however, most embryo rescue is accomplished 16 to 18 days after pollination.

There is a range of endosperm and embryo development in wide hybrids which is cross-dependent. The fortuitous combination of the appropriate genotypes of the male and female gametes required for successful embryo development in attempted wide hybrids produces anomalies in any type of classification of embryo and endosperm development. For example, the many pollinations made to produce the hybrid *T. timopheevii* x *Hordeum bogdanii* (Kimber and Sallee, 1976; and Sallee, unpublished) resulted in only one seed which had a normal embryo and endosperm and which matured on the plant. In addition the production of hybrids is strongly affected by environmental conditions. It is possible to classify embryo development into normal, reduced and tiny; and endosperm development into normal, reduced and watery. Normal embryo development is found in essentially all intraspecific hybrids but less frequently in interspecific and very rarely in intergeneric hybrids. Reduced embryos are classified as those in which a small shoot, radicle and scutellum can be identified, while tiny embryos are those prior to this level of differentiation. Normal endosperm is milky early in development, becomes floury as development proceeds and eventually results in a dry, plump seed. Reduced endosperm passes through all the normal stages of development but if left to develop to maturity the grain is small and shrivelled. The classification watery endosperm is used to describe those cases where the endosperm does not even develop to the milk stage. Examples of hybrid combinations that resulted in mature plants derived from this range of embryo and endosperm development are given in Table 1.

The development of new media will undoubtedly allow the recovery of even younger and more poorly developed embryos. This is an area of study that currently seems to be attracting little attention, yet the potential of increasing the range of wide hybrids that may be produced is substantial. The difficulty of producing mature plants from hybrids of only a few cells is probably considerably less than from artificially fused somatic cells because some level of compatibility has already been demonstrated by the fact that sexual fusion has taken place. It would seem, therefore, that the improvement of embryo-rescue techniques would present a greater potential of utilizing the alien genetic material found in distant, but related species, than would somatic-cell fusion.

Endosperm	Embryo	Female Parent	Male Parent
Normal	Normal	T. timopheevii	H. bogdanii
		T. aestivum	A. intermedium
Reduced	Normal	T. aestivum	T. umbellulatum
Reduced	Reduced	T. tauschii	T. aestivum
Watery	Reduced	T. aestivum	A. campestre
		T. aestivum	A. curvifolium
Watery	Tiny	T. aestivum	A. repens
		T. aestivum	E. angustus

Table 1. Examples of endosperm and embryo development in successful wide hybrids in the **Triticeae**.

CYTOLOGY

Since characters of generic importance may be entirely suppressed in wide hybrids (Kimber 1983), the morphological recognition of hybrids can be very unreliable. A convincing demonstration of hybridity can only be made by cytological investigation, and then it is possible to come to erroneous conclusions even if a detailed meiotic analysis is made. The difficulties hindering the positive cytological identification of hybrids tend to be of four types: first, technical problems in the collection and preparation of material; second, unreliability of the cytological technique chosen; third, somatic chromosome elimination or chimeras; and fourth, misinterpretation of meiotic data.

The collection of root tips from a hybrid for cytological analysis is usually delayed until the hybrid is growing in a plant pot because of the small number (often only one) of roots produced in culture. When roots are taken from pots, the number of dividing cells is usually less than that found in germinating normal seedlings in a petri dish. Further, silica particles adhering to the roots can spoil the preparation of good squashes. Nevertheless, root tip preparations from plants in pots can provide the first indication of hybridity. Feulgen or carmine staining of prefixed cells will provide a chromosome count that can eliminate accidental self-pollinations. A new technique (Mujeeb-Kazi and Miranda, 1985) can result in very clear preparations from which not only chromosome number may be determined but arm ratios, secondary constrictions and intergeneric differences in chromatid thickness (e.g. **Agropyron/Secale**.) can be identified. If both parents of a hybrid have the same chromosome number, somatic chromosome counts, at the best, can only give an indication of hybridity if there are large and characteristic karyotypic differences between the parental species.

The reliability of the chosen cytological technique must also be considered in the recognition of hybridity. Simple counting of somatic chromosome number, if the parents differ in their chromosome number, can be reliable. If the somatic chromosome numbers are the same, it is still possible that the parents differ in their ability to C- or N-band. The reliability of the recognition of hybridity on the basis of chromosome banding is directly proportional to the number, intensity and chromosomal distribution of the bands. If the arm ratio of the chromosomes of the parents is sufficiently different, this too may be used as an indication of hybridity. Again the reliability of arm ratio as a pointer to hybridity depends on the number of easily recognized differences between the parents. The presence or absence of secondary constrictions is not a good method of recognizing hybrids. First it requires that superior somatic preparations must be made, and second no nucleolar organizer competition must take place. The length of somatic chromosomes generally provides a very poor method for the identification of hybridity. The general absence of large differences in relative length in the **Triticeae** and the inaccuracy involved in making measures of length (Kimber, 1970) both contribute to a low reliability.

Even if an interspecific or intergeneric hybrid zygote is recovered, it is possible that the seedling may not be hybrid, due to chromosome elimination in the early zygotic divisions. The production of haploid barleys and wheats as a consequence of pollination by **Hordeum bulbosum** is an example of this type (Kasha and Kao, 1970; Barclay, 1975). The spontaneous production of chimeras may also hinder the recognition of hybrids or make the utilization of them more difficult. Chimeras have been recognized by several authors; for example, Kasha and Sadasivaiah (1971) recorded the expected chromosome number in only 40 per cent of the somatic cells of a diploid hybrid of **Hordeum vulgare** x **H. bulbosum**. Also, Kimber (unpublished) has recovered a haploid/diploid chimera instead of a hybrid following pollination of wheat by a related diploid. The origin of such plants is, of course, obscure because there is no proof of hybridity or the tissue from which the embryo actually developed.

Clearly, when such difficulties abound, any claim of hybridity must be accompanied by clear meiotic analyses. Since both the determination of species relationships and the choice of the most suitable method for the introduction of alien variation depend on the ability of the chromosomes to pair, the interpretation of meiotic analyses is of some importance. In the earliest work the judgements were largely subjective, but essentially correct conclusions were reached (see Lilienfeld 1951). More recently numerical methods for the analysis of meiosis in hybrids have provided some objectivity in determining genomic relationships (Kimber *et al.* 1981, Alonso and Kimber 1981, Kimber and Alonso 1981, Espinasse and Kimber 1981, Kimber and Pignone 1982).

Ideally genomic analysis is conducted in a triploid hybrid between a tetraploid and a diploid analyser; however analyses are often made at other polyploid levels. In general, diploid hybrids can provide little if any genomic information, for there must be competition for chromosome pairing partners in order to recognise differences in the genomes present. The pairing patterns at higher levels of polyploidy can be very confusing because of the large number of pairing possibilities between both the homologous (if present) and homoeologous chromosomes within any homoeologous group. These practical limitations result in a useful range of triploid to pentaploid hybrids from which information can be reliably obtained. If telocentric chromosomes are available, they can provide unequivocal information about the frequency with which particular chromosomes are pairing, but their usefulness is usually limited to measurements of relationships with the A, B and D genomes of *T. aestivum*.

In general, clear proof of hybridity can only come from the meiotic analysis of hybrids. The investigation of species relationships from back-crossed hybrids can, in some cases, be accomplished; however, complications introduced by the production of unreduced gametes or the random elimination of chromosomes can give rise to incorrect interpretations.

PRACTICALITY

Since the introduction of the *Lr9* locus from *T. umbellatum* by Sears (1956), most of the examples of the introduction of alien variation involve loci for disease reaction. Recently Avivi (1979) has described the introduction of genes affecting protein content from *T. dicoccoides* into *T. aestivum*. There is a qualitative difference between the interactions of the two types of introduced genetic material that is of considerable significance. In all cases involving disease reactions both the introduced genetic material and the genetic material of the pathogen are free to mutate; consequently the durability of usefulness of the alien material is limited by the natural variation of the pathogen. The introduction of alien genetic material affecting physiological traits of the recipient species is free from this restriction. The two types of system can be described as dynamic and static. In a dynamic system it is to be expected that the introduced variation would have a durability no greater than genes available by intraspecific manipulation. In this respect they should be

considered no differently than the other genes manipulated by conventional plant breeding methodology. However, in the case of Karnal Bunt resistance it would seem that there is no available source of resistance in the cultivated forms and therefore the loci located in the wild relatives have an increased desirability even though their ultimate practicality will be limited by the constraints of a dynamic system. Genes in a static system are not subject to this limitation; consequently manipulations introducing material of this type have the potential of producing breakthroughs in commercial production. It would be anticipated, for example, that if it is possible to introduce genetic material providing drought resistance or tolerance, high protein content, protein quality, salt tolerance or various metal tolerances, wheat could then be cultivated in areas where this is currently impossible or impractical.

Most of the introduced loci have been initially placed in the cultivar Chinese Spring. This is a consequence of the use of this variety in the production of the essentially complete range of aneuploids (Sears, 1954; and Sears and Sears, 1978) and also its ease of crossability. Its agronomic characteristics are, however, totally unacceptable. The ease of hybrid production in this cultivar is mainly a result of the presence of *kr1* and *kr2*, the crossability genes (Riley and Chapman, 1967). Other varieties of greater commercial acceptance have now been identified with the recessive genes at these loci (Mujeeb, unpublished) and in addition a third homoeo-allele (*kr3*) has been reported (Falk and Kasha, 1981; Fedak and Jul, 1982) in Chinese Spring and it may be anticipated that it will also be present in other varieties. The use of agronomically acceptable varieties for the initial hybridization should now remove the requirement for many generations of backcrossing needed following hybridization of distant relatives with the cultivar Chinese Spring.

The phenotype of wide hybrids and their derived amphiploids mitigates against their commercial use; consequently additional cytogenetic manipulations must be made before practical application becomes possible. In general these manipulations will be directed at introducing the smallest piece of genetic material capable of controlling the desired phenotype without affecting the other essential attributes of the recipient species.

The closeness of phylogenetic relationship, the ease of hybridization and a high recombination frequency of the donor and recipient chromosomes are all manifestations of genetic commonality of the two species. Consequently it is to be expected and has been observed, that the majority of the introductions of alien variation in the *Triticeae* have been accomplished by recombination.

As phylogenetic distance increases so does the difficulty of the introduction of alien variation. Kimber (1984a) has described a rationale for the selection of the appropriate technique for the introduction of alien variation based on measurements of the relative affinity and mean arm-pairing frequency of the chromosomes involved. As the genomic relationships decrease it first becomes necessary to induce recombination by manipulations of the chromosome-pairing regulator systems, and when the relationships are so remote that this is not possible, it is essential to resort to methods causing the breakage and reunion of chromosomes.

Sharma and Gill (1983) have published an extensive list of hybrids involving species of the *Triticeae* and also many examples of desirable genes transferred from wheat relatives into *T. aestivum*, most of which are now in commercial varieties. Consequently there can be little doubt about the practicality of the introduction and usefulness of alien variation.

DISCUSSION

It is now over 25 years since Sears (1956) introduced the *Lr9* gene from *T. umbellulatum* into *T. aestivum* by irradiation, and in this time the range and potential of the techniques available for this type of manipulation have increased considerably. This improvement has been both in the production of wide hybrids and in the cytogenetical manipulations possible on the derivatives of the hybrids.

Most of the species of the former genus *Aegilops* can now be hybridized, almost at will, with the cultivated wheats. Their genomic relationships are well understood and recent work has further elucidated the situation (Kimber, 1984b). Once desirable variation has been recognized in the wild species and its epistasis in a hybrid is established, then the choice of methodology for the introduction of the alien variation follows logically from measurements of the relative affinity of the chromosomes involved. This ability can only greatly increase the range of variation upon which plant breeders can exercise selection.

Hybrids and, in most cases, amphiploids have been produced between species of the genera *Hordeum*, *Agropyron*, *Elymus*, *Secale*, *Taeniatherum*, *Eremopyrum*, and *Haynaldia* and various species of the genus *Triticum* as defined by Morris and Sears (1967) (Sakamoto, 1973; Mujeeb-Kazi, 1982 and Sharma and Gill, 1983). The range of new hybrids with more distantly related species is constantly increasing and it is to be expected that a greater range of genotypes will become available for introduction.

As the demands for increased world food production increase, the value of introduced variation will also increase. It is not possible to predict the future genetic demands that may be placed on wheats as new races of pathogens appear or as cultivation is extended into new areas; consequently a stock of alien genetic material introduced from wide hybrids may prove to be of great value.

The practical potential of wide hybridization in the *Triticeae* is probably greater than in most other groups, partly because of the ease of hybridization, partly because of the extensive existing cytogenetical understanding and partly because of the immense importance of the wheat crop. Consequently there may not be as much need to utilize techniques such as gene splicing or somatic cell fusion as in other crops. Further, such techniques may have limitations in that the introduced material may not integrate well with the wheat genotype. The introduction of genetic material from species with relatively close evolutionary ties to wheat would, a priori, be expected to have the most potential. In addition, the

ability to induce recombination between homoeologous chromosomes in this group would tend to place introduced segments in the best location in the recipient chromosomes.

It would appear that the use of wide hybrids and the derived genetic material in the *Triticeae* will provide an expanding source of genetic variation for the plant breeders which, in some cases, may even amount to quantum changes in either the production or distribution of the crop.

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VARIATIONS IN MEIOTIC PATTERNS AND POLLEN FERTILITY OF THE WHEAT-RYE POLYHAPLOIDS

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Summary

Meiosis was studied in the ABDR F_1 polyhaploid hybrids *Triticum aestivum* L. var. Saratovskaya 29 x *Secale cereale* L. var. Onohoiskaya. It was found that the hybrids have different meiotic patterns and pollen fertility.

The results obtained allowed us to explain the nonreduction of chromosome number in the viable gametes of polyhaploids ABDR as follows: 1) viable gametes are predominantly formed in those ABDR plants in which the number of homoeologous bivalents is, in the majority, small, the univalents divide equationally, and the chromosomes do not segregate at anaphase II; 2) the formation of viable gametes with different chromosome combinations of the four genomes of the ABDR F_1 hybrids is unlikely, when homoeologous pairing is low, division of univalents at anaphase I equational, and poleward passage at anaphase II random.

Index words: Intergeneric hybrids - Homoeologous pairing - Chromosome segregation - Karyotype evolution.

Introduction

Our previous results indicated that karyotype stabilization in hybrids with a haploid set only gives rise to amphiploids (Shchapova and Kravtsova 1982; Shchapova et al. 1984). These results were contrary to expectation because these polyhaploids should produce forms with reconstructed genomes.