Reprinted from

WHEAT INFORMATION SERVICE

No. 55 September, 1982

Wheat Information Service
Kihara Institute for Biological Research
Yokohama, Japan

Unexpected chromosome numbers in backcross I generations of F_1 hybrids between *Triticum aestivum* and related alien genera

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Self-sterile F_1 hybrids within the *Triticinae* are often partially female fertile. This allows successive generations to be obtained by backcrossing the F_1 hybrid to a common wheat parent with the eventual isolation of individual addition lines of the alien species as described by O'MARA (1940). The reason for the partial female fertility has been assumed to be due to the formation of unreduced female gametes.

The expected chromosome number in the first backcross generation (BC_1), based on the premise of unreduced eggs being the only functional gametes, has not been uniformly achieved.

MUJEEB-KAZI & BERNARD (1982) found a variation in chromosome numbers in BC_1 progenies involving *Agropyron*, *Triticum aestivum*, *T. turgidum* and *Elymus* species hybrids, as did PIENAAR for *T. aestivum*/*A. distichum* (1980).

An explanation has been offered for only some of these unexpected chromosome numbers. For example, apomixis (MUJEEB-KAZI 1981), chromosome elimination of the alien genome, and spontaneous doubling have been used to explain unexpected numbers of exact multiples of the expected. The derivation of the many other observed chromosome numbers has not been explained, possibly due to complexities involved in determining chromosome identification.

GERLACH (1977) demonstrated that 9 of the 21 wheat chromosomes could be identified using the N-banding technique. JEWELL (1979) confirmed the N-banding of wheat chromosomes and demonstrated that all 14 chromosomes of *Aegilops variabilis* also exhibited unique N-banding patterns which enabled them to be identified and differentiated from wheat chromosomes. The hybrid of *T. aestivum* cv. Chinese Spring and the tetraploid *Ae. variabilis* usually exhibits 35 univalents at metaphase 1 and there is less than 1 chiasmata per cell (DRISCOLL & QUINN, 1968). These plants are self-sterile. Therefore, the BC_1 plants should provide excellent material for chromosome analysis.

The technique used for N-banding analysis is described in detail by JEWELL (1981). However, for ongoing studies at CIMMYT, due to high altitude (above 2,225 m), it was necessary to adjust the technique because the normally used temperature of the acid buffer ($92° \pm 1°C$) is not obtainable. At $87°C \pm 1°C$ it requires 46 to 50 minutes in 1M NaH_2PO_4 buffer to produce good bands. However, the chromosome morphology is adversely affected

The research on the backross plants of Chinese Spring by *Aegilops variabilis* was undertaken while the senior author was at the Waite Agricultural Research Institute, University of Adelaide, Australia. Reprints may be requested from A. Mujeeb-Kazi.

by this length of treatment. Hence, it was more satisfactory to use 2M NaH_2PO_4 buffer for 25–28 minutes at 87 ± 1°C. Apart from this, the technique was the same as previously described (JEWELL 1981).

Table 1. Chromosome numbers observed in 20 BC_1 plants of (*Triticum aestivum* cv. Chinese Spring/*Aegilops variabilis*)//*T. aestivum* cv. Chinese Spring.

Chromosome No.	39	40	43	46	47	50	53	54	56	59	63
No. of plants	1	1	1	1	1	1	2	4	6	1	1

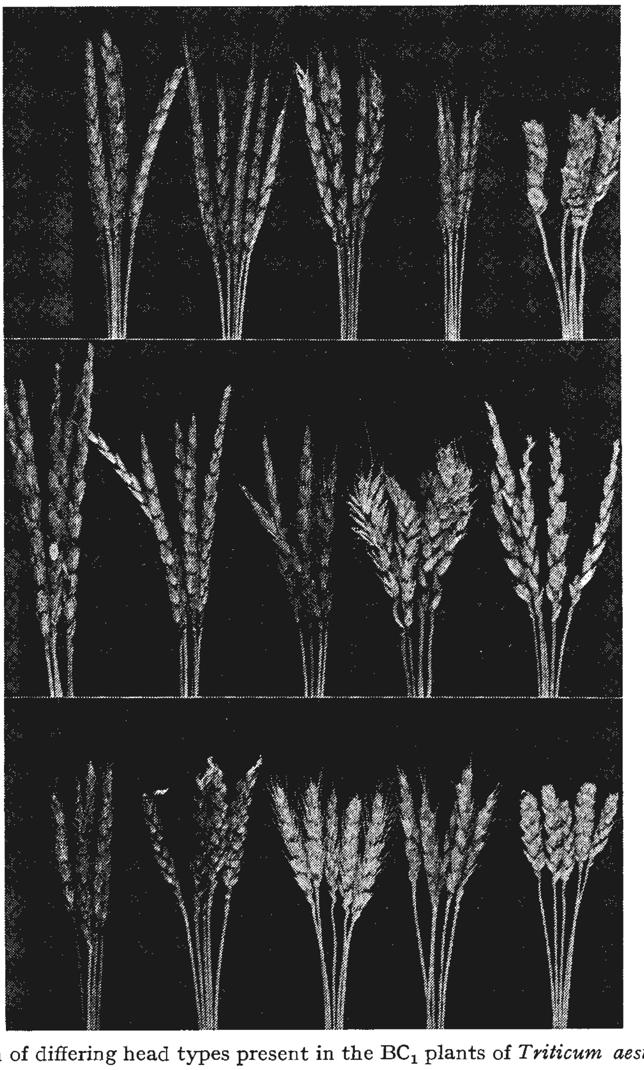

Fig. 1. A selection of differing head types present in the BC_1 plants of *Triticum aestivum* cv. Chinese Spring/*Aegilops variabilis*/ /*T. aestivum* cv. Chinese Spring. Each of the 15 examples of head type were from different BC_1 plants. The first five examples of head type were all taken from BC_1 plants containing the expected chromosome number of 56.

The F_1 of Chinese Spring and *Ae. variabilis* has 35 chromosomes (21 from wheat and 14 from *Ae. variabilis*). Therefore, the expected number in the BC_1 plants derived using pollen from Chinese Spring would be 56 (35 from the unreduced female gamete and 21 wheat chromosomes from the pollen parent). Twenty BC_1 seeds were randomly chosen for chromosome analysis using N-banding, and a range of chromosome number was observed between 39 and 63 (Table 1).

The aim of the analysis was to use N-banding to determine whether there were changes in the chromosome numbers of wheat, or *Ae. variabilis*, or changes in both chromosome complements in the BC_1 plants. Further, MUJEEB-KAZI (1981) has postulated that the meiosis of the F_1 plants must be slightly irregular in order to give rise to the unexpected numbers. The authors explored the possibility that partially reduced eggs may function producing BC_1 progeny of varied chromosome number.

N-banding analysis of the Chinese Spring/*Ae. variabilis* F_1 backcrossed to Chinese Spring demonstrated the following points:

i) At least 1 representative of the N-banded wheat chromosomes was always present.
ii) Some triplication of N-banded wheat chromosomes and some duplication of *Ae. variabilis* chromosomes were observed.
iii) The loss or duplication of chromosomes appeared to be random.
iv) The 56 chromosome plants did not have the expected 18 banded wheat chromosomes and 14 *Ae. variabilis* chromosomes, and their spike/morphology was different (Fig. 1).

The presence of one representative of each of the N-banded wheat chromosomes is expected from the pollen parent, and was observed. Thus, it would appear that partially reduced F_1 female gametes are indeed functional. The partially reduced gametes are assumed to result from random movement of univalents to the poles at anaphase 1 which is the normal occurrence when chromosomes do not have a homologue with which to pair. Further, the duplication of *Ae. variabilis* chromosomes and the triplication of wheat chromosomes are presumed to have arisen by division of the chromosome(s) involved at metaphase 1, followed by movement of both chromatids to the same pole.

Fig. 2 shows the N-banded karyotype of a 39-chromosome BC_1 plant of Chinese Spring/*Ae. variabilis*//Chinese Spring. If, as proposed above, the pollen contributes 21 chromosomes (9 banded and 12 unbanded), (the authors infer that) the functional female gamete had 18 chromosomes. Due to N-banding analysis, these 18 chromosomes can be grouped as follows: 4 of the expected 9 N-banded wheat chromosomes, 7 of the 14 *Ae. variabilis* chromosomes (one of which is duplicated, thus totaling 8 chromosomes) and, by inference, 6 of the 12 unbanded wheat chromosomes. The 6 unbanded wheat chromosomes may, of course, include duplicates. The results indicate that no one genome present in the F_1 is being preferentially excluded from the female gamete. To the best of our knowledge, these findings offer an explanation of unexpected numbers by assuming that some partially reduced gametes, formed by random movement of univalents to poles of anaphase 1, are functional, this being enhanced by the polyploid nature of the material.

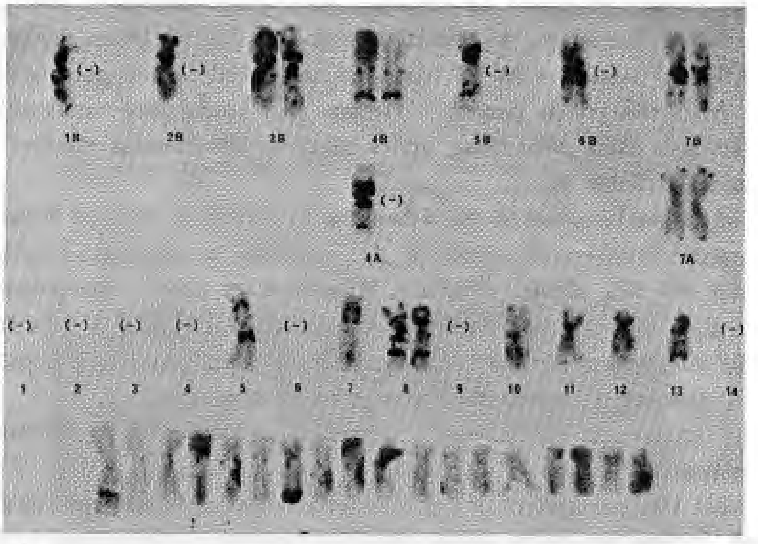

Fig. 2. The N-banded karyotype of a BC_1 plant (*Triticum aestivum* cv. Chinese Spring/*Aegilops variabilis*//*T. aestivum* cv. Chinese Spring) containing 39 chromosomes rather than the expected 56 chromosomes.

Some of these BC_1 plants are partially self-fertile and it is envisaged that, through selfing, novel combinations of chromosomes can be obtained; for example, several homoeologous and non-homoeologous substitutions of alien chromosomes in the one plant. These plants may be useful in plant breeding programs.

It has been demonstrated that hexaploid wheat, which is nullisomic for chromosome 5B, will exhibit a considerably increased amount of pairing between homoeologous chromosomes (RILEY & CHAPMAN 1958; SEARS & OKAMOTO 1958). This increase in homoeologous pairing may result from a greater similarity of sites for crossing over and is maximized in hybrids because of the absence of strict homologues (DRISCOLL *et al.* 1979)

Since some of the partially self-fertile BC_1 plants are monosomic for chromosome 5B, selfing of these plants is expected to give rise to plants deficient for chromosome 5B. The plants deficient for chromosome 5B should allow exchange of genetic material between wheat and homoeologous alien chromosomes. Further, it is possible that these plants may give rise to more genetic exchanges between wheat and the alien genera because of the expected higher level of univalency than in some other systems of using modifications of chromosome 5B.

Initial N-banding studies of the chromosomal complement of BC_1 plants of *T. aestivum*/*A. elongatum*//*T. aestivum*, which exhibit unexpected numbers (RODRIGUEZ & MUJEEB-KAZI, 1981), have also disclosed a similar phenomenon; it appears that these numbers arise from a partially reduced egg cell, pollinated by normal wheat pollen (MUJEEB-KAZI & JEWELL, unpublished). Work is continuing in order to generalize this hypothesis for the *Triticinae*.

Acknowledgements

We are grateful to Professor C.J. Driscoll for his valuable criticism and advice on the manuscript and to Mrs.A. Povich, for editorial contributions.

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