SHORT PAPERS

The addition of the chromosomes of *Aegilops* *umbellulata* to *Triticum aestivum* (var. Chinese Spring)

By GORDON KIMBER

Plant Breeding Institute, Trumpington, Cambridge

The collection of complete sets of lines with the separate disomic addition to *T. aestivum* of each chromosome of an alien diploid genome has been limited to the genera *Agropyron*, *Secale* and *Haynaldia* (Riley & Kimber, 1966). The more closely related genus *Aegilops* has but scant representation in the literature dealing with the alien chromosome addition.

It is possible, because of the closer genetic equivalence of the *Aegilops* chromosomes to those of the hexaploid wheats, that occasional synapsis and recombination may occur between wheat and *Aegilops* chromosomes and thus destroy the genetic integrity of the alien chromosome that is required for the isolation and maintenance of stable addition states.

It seems, however, that in the case of *Ae. umbellulata* the meiotic isolation is complete and the problem of producing addition sets stems from the difficulty of making the initial intergeneric hybrid. Sears (1956) overcame this problem by crossing the amphiploid of (*T. dicoccoides* × *Ae. umbellulata*) to *T. aestivum*. However, this technique will always be open to the objection that any phenotypic modification of the wheat recipient due to the presence of an *Ae. umbellulata* chromosome may be masked by the failure to reconstruct the genotype of *T. aestivum*. The repeated backcrossing of this amphiploid or its derivatives to *T. aestivum*, while improving the genetic restoration of the background, would be a most laborious and usually an incomplete process.

When *T. aestivum* ($2n = 6x = 42$) var. Chinese Spring was pollinated by *Ae. umbellulata* ($2n = 2x = 14$) in the present experiments, seed, usually with a shrivelled endosperm, was produced in 0 to 95% of the pollinations. This seed, however, always failed to germinate. The embryos of the dry seed were easily removed and cultured, with a high percentage of success, on nutrient agar (Kimber, 1961). The hybrids were small, stunted and completely sterile. The colchicine-induced amphiploid was small, many tillered and produced a low percentage of seed, few of which germinated. Following the first backcross to Chinese Spring the viability, vigour and fertility of the offspring were rapidly improved. Further backcrosses, using wheat as the recurrent pollen parent on to the forty-nine chromosome plant (21″ wheat + 7′ *umbellulata*), produced progeny with chromosome numbers ranging from 42 to 49 and the selection of monosomic additions (21″ wheat + 1′ *umbellulata*) was relatively simple. The production of disomic additions by self-pollinating the monosomic additions follows and so far six of the seven possible disomic additions have been isolated. The pedigree of this material is given in Text-fig. 1.

The addition lines were designated by letters in order to avoid confusion of the numbers of the chromosomes they carry with those of the wheat homoeologous groups and to allow the chromosomes to be re-numbered if it is possible to recognize the homoeologous group to which they can be ascribed.

Six of the chromosomes of *Ae. umbellulata* are distinct from the chromosomes of *T. aestivum* (Plate I). Two are satellited (B and C) and are distinct from each other and

from the wheat-satellited chromosomes (1B and 6B). Four of the *Ae. umbellulata* chromo-somes have sub-terminal centromeres (A, D, E and G). The remaining chromosome of *Ae. umbellulata,* so far not isolated as an addition, has a sub-median centromere and is not distinguishable from nineteen of the wheat chromosomes. The chromosome con-figuration at first meiotic metaphase of the monosomic addition lines was generally twenty-one bivalents and one univalent. The *Ae. umbellulata* univalent was not observed to pair with a wheat chromosome in any of the six lines examined, neither was there any noticeable increase in the failure of the wheat chromosomes to make bivalents. All of the disomic addition lines had a first meiotic metaphase configuration of twenty-two bivalents and, as was observed in the monosomic addition lines, no disturbance of the normal pairing pattern of the wheat chromosomes was recorded. This meiotic pattern resulted in the majority of the self-pollinated progeny of the disomic addition lines having the chromosome constitution of their parent, only occasionally where the alien chromosomes had failed to pair were forty-three chromosome monosomic addition progeny recovered.
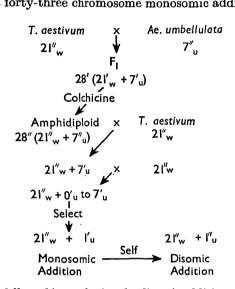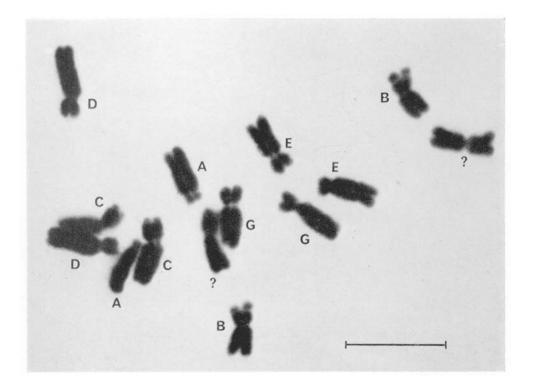
$$T.\ aestivum \quad \times \quad Ae.\ umbellulata$$
$$21''_w \quad\quad\downarrow\quad\quad 7''_u$$
$$F_1$$
$$28'\ (21'_w + 7'_u)$$
$$Colchicine$$
$$Amphidiploid \quad \times \quad T.\ aestivum$$
$$28''\ (21''_w + 7''_u) \quad\quad 21''_w$$
$$21''_w + 7'_u \quad \times \quad 21''_w$$
$$21''_w + 0'_u\ to\ 7'_u$$
$$Select$$
$$21''_w\ +\ 1'_u \quad\quad 21''_w\ +\ 1''_u$$
$$Monosomic \xrightarrow{\ Self\ } Disomic$$
$$Addition \quad\quad\quad Addition$$

Fig. 1. The pedigree followed in producing the disomic addition of single chromosomes of *Ae. umbellulata* to *T. aestivum* (′ represents univalent, ″ bivalent).
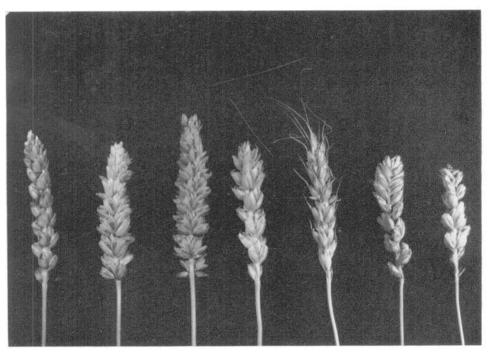
Phenotypically the disomic additions differ from Chinese Spring in several respects (Table 1 and Plate II). Perhaps the most divergent phenotypes are those of disome C which is about 40 cm. shorter than Chinese Spring, which was about 100 cm. high, and disome D which is awned. Disome A carries, on the long arm of the chromosome, a gene or genes conferring resistance to brown rust (*Puccinia recondita*), and disome G carries, also on the long arm of the chromosome, a gene or genes affecting the time of flowering and maturity. With the exception of the disomic addition of *Ae. umbellulata* chromosome C the fertility of the addition lines was very similar to that of the recipient variety Chinese Spring. Disomic addition lines of chromosome C had a reduced fertility.

This set of addition lines is interesting in several respects. For example, it may be possible to use them to obtain some indication of the evolutionary processes that were responsible for the sub-terminal position of four of the centromeres of the *Ae. umbellulata* chromosomes. Throughout the genera *Triticum* and *Aegilops* the centromere is generally sub-median in position and this is widely considered to be the primitive state. The sub-terminal centromeres of some chromosomes of some species in the genus *Aegilops* have arisen by structural alterations. Since *Ae. umbellulata* is a diploid species and four of its

The somatic chromosomes of *Ae. umbellulata*. The chromosome marked with a question mark has not yet been isolated as an addition to *T. aestivum*. Scale = 5μ.

From left to right. Ears of Chinese Spring and disomic additions of single chromo-
somes A, B, C, D, E and G of *Ae. umbellulata* to Chinese Spring.

chromosomes have sub-terminal centromeres it is improbable that this centromere position has resulted from the terminal deletion of most of a chromosome arm. The loss of this amount of genetic material would almost certainly be lethal to a diploid organism. Furthermore, if the sub-terminal centromere position had resulted from terminal deletion then it would be expected that these chromosomes would be amongst the shortest in the complement. The two longest chromosomes of the *Ae. umbellulata* complement are D and G, both of which have sub-terminal centromeres. Therefore, it seems that the cytological processes involved in this movement of the centromere must have been either intra-chromosomal or inter-chromosomal. If they were intra-chromosomal, for example involving unequal pericentric inversions, then while the distribution of the genes on the chromosomes is re-patterned the total genetic content remains unaltered. However, if the processes were inter-chromosomal, for example two unequal

Table 1. *The chromosome type and phenotype of the six disomic addition lines of* Ae. umbellulata *chromosomes to* T. aestivum

Addition	Chromosome	Phenotype of disome
A	Sub-terminal	Ear like Chinese Spring. Brown rust resistance determined by the long arm of chromosome.
B	Satellited	Ear longer than Chinese Spring.
C	Satellited	Ear short and lax, with fewer spikelets than Chinese Spring. Plant height ± 40 cm. less than Chinese Spring.
D	Sub-terminal	Awned, plants with the long arm telocentric alone are awned, therefore the gene concerned is not on short arm.
E	Sub-terminal	Ear shorter than Chinese Spring. Plant height ± 20 cm. less than Chinese Spring.
G	Sub-terminal	Late flowering determined by the long arm of chromosome. Ear shorter and with fewer spikelets than Chinese Spring.
?	Sub-median	?

reciprocal translations, then the genes would be re-distributed between the two or more chromosomes involved.

Sears (1965) showed, by nullisomic–tetrasomic compensation techniques how the twenty-one chromosomes of *T. aestivum* could be classified both by origin and function into seven groups of three. This division was such that one member of each group of three (homoeologous group) came from each of the three genomes that are present in *T. aestivum*. Knott (1964), Riley (1964) and Johnson (1966) expect that it will also be possible to incorporate alien chromosomes in this homoeologous grouping. Johnson, for example, showed that a particular *Agropyron* chromosome would only substitute for chromosomes of wheat homoeologous group six, while Riley was only able to substitute chromosome II of *Secale cereale* for the chromosomes of wheat homoeologous group six. Thus the ability of an alien chromosome to be matched against the wheat homoeologous grouping depends on the genetic equivalence of the alien chromosome to the wheat group.

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Therefore, if the sub-terminal positions of the centromere on chromosomes A, D, E and G of *Ae. umbellulata* have arisen by intra-chromosomal changes then each of these chromosomes should compensate for a different wheat homoeologous group. However, if the change involved inter-chromosomal processes then each chromosome should compensate only partially for more than one homoeologous group. Attempts to substitute these chromosomes for all the wheat chromosomes, so that their compensating ability can be evaluated, are being made at the present time.

A second point of interest in the addition of the chromosomes of *Ae. umbellulata* to *T. aestivum* is that by the method used the genetic variation of the background is minimal. This was achieved by making the original and all subsequent crosses to a single wheat variety (Chinese Spring) that has been maintained by selfing for many years. This feature of the additions allows attempts at the translocation of alien variation to wheat chromosomes to proceed without the creation of a heterozygous and therefore segregating background.

Finally, since it is possible (Kimber, unpublished) to induce at least chromosome A of *Ae. umbellulata*, which causes brown rust resistance, to recombine with a wheat chromosome in the absence of wheat chromosome 5B, then comparisons of the efficiency of irradiation and recombination methods for the introduction of alien variation into *T. aestivum* are possible.

SUMMARY

Six lines have been isolated in which individual chromosomes of *Ae. umbellulata* have been added to the normal complement of *T. aestivum*. The phenotype and cytology of these lines and of the material employed in their production is briefly described. The use of some of these lines in investigations on the evolution of the diploid *Aegilops* species and in the introduction of useful alien variation into *T. aestivum* is mentioned.

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