# CHROMOSOME PAIRING IN A NULLI-5B DI-5D WHEAT HAPLOID\*

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Common wheat (Triticum aestivum L. emend. Thell. subsp. vulgare) normally behaves as a strict allohexaploid forming only bivalents at meiosis. Chromosomes of homoeologous group 5, particularly 5B and 5D, are important in the genetic regulation of this behaviour. The failure of homoeologous chromosomes to pair is due to the pairing suppression shown by chromosome 5B (Riley 1960). In part the evidence is that nulli-5B haploids exhibit a high degree of bivalent and multivalent associations (Kimber and Riley 1963). Riley (1960) found that 5B interferes with processes leading to synapsis. Riley, Chapman, and Kimber (1960) located this activity on the long arm of 5B (5B<sup>L</sup>). Feldman (1966) concluded that it regulates premeiotic chromosome association. Further he found that, although six doses of 5D<sup>L</sup> have no observable meiotic effect, nullisomic-5D plants are partially asynaptic. However, they exhibit homoeologous pairing with interlocked bivalents and he concluded that 5D carries a gene increasing premeiotic association and hence that its effect is opposite to that of 5B. Riley (1966) also reported that in nulli-5D tetra-5B plants there is considerable reduction in metaphase chiasmata frequencies at low temperatures. From a comparison with tetrasomic-5B individuals he suggested that this reduction is due to the deficiency of chromosome 5D which implies that 5D carries a gene(s) which stabilizes meiotic pairing against variations due to temperature differences. From chiasmata frequencies per chromosome at different temperatures in plants with varying doses of homoeologous group 5 chromosomes Rilev et al. (1966) confirmed that chromosome 5D is vital for the maintenance of normal synapsis at low temperatures.

One of twin-embryo seedlings from a cross between a Chinese Spring nulli-5B tetra-5D plant and a wheat line (2n = 44) carrying a pair of Agropyron elongatum (Host.) Beauv. telocentric chromosomes which conferred resistance to stem rust (*Puccinia graminis* var. tritici Eriks. & E. Henn.) had 43 chromosomes as expected. It was rust resistant due to the Agropyron telocentric chromosome and was presumably mono-5B tri-5D in constitution. At meiosis it invariably exhibited at least one bibrachial univalent (comprising or including the mono-5B chromosome) and usually a trivalent (apparently an association of the three homologous 5D chromosomes). Occasionally a quadrivalent was present, sometimes in addition to a trivalent, indicating a chromosome translocation difference between Chinese Spring and the varietal background to which the telocentric Agropyron chromosome had been added.

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The second twin-embryo plant proved to be a rust susceptible haploid with 21 chromosomes. From its parentage and the meiotic behaviour of the sister hybrid plant it was presumably nulli-5B di-5D in constitution. At the haploid level pairing potentialities are obviously accentuated by the absence of homologous chromosomes (except in the case of 5D in the present instance). This is shown in Table 1 which includes previously reported data on typical metaphase I meiotic associations in certain euhaploid and nulli-5B haploid plants of T. aestivum. Although multivalent associations are extremely rare in euhaploid plants in the absence of structural hetero-zygosity, the presence of one or more bivalents is usual in euhaploids and trivalent associations are recorded.

#### TABLE 1

METAPHASE I MEIOTIC CHROMOSOME ASSOCIATIONS IN VARIOUS EUHAPLOID, NULLI-5B HAPLOID, AND NULLI-5B DI-5D HAPLOID PLANTS OF TRITICUM AESTIVUM

I= univalents,  $II_{o}=$  open or rod bivalents,  $II_{c}=$  closed or ring bivalents; III= trivalents, IV= quadrivalents

| Designation             | Mean Associations     |  |  |                |                                       |
|-------------------------|-----------------------|--|--|----------------|---------------------------------------|
|                         | I                     | IIo  | IIc  | III            | IV                                    |
| Euhaploid*              | 19.18                 | 0.89   | 0.005  | 0.008          | · · · · · · · · · · · · · · · · · · · |
| ${f Euhaploid}\dagger$  | $17 \cdot 14$         | $1 \cdot 48$   | $0 \cdot 105$  | 0.03           |                                       |
| Nulli-5B haploid*       | 7.83                  | 4.55   | 0.65   | 0.53           | $0 \cdot 02$                          |
| Nulli-5B di-5D haploid‡ | $8 \cdot 01 \ (4-13)$ | $\begin{array}{ c c c } 2 \cdot 63 \\ (0-6) \end{array}$ | $\begin{array}{c c} 2 \cdot 90 \\ (1-6) \end{array}$ | $0.65 \ (0-3)$ | 0·01<br>(0-1)                         |

\* Data of Kimber and Riley (1963).

<sup>†</sup> Data of E. R. Sears (personal communication).

<sup>†</sup> Range of values in parenthesis.

In the nulli-5B di-5D haploid plant an opportunity was afforded of studying, at this level of ploidy, the effect on chromosome associations of two doses of 5D in the absence of the homoeologous 5B chromosome. The results are incorporated into Table 1 and show a high degree of multivalent and bivalent associations at meiosis due to the removal of the pairing suppression effect of 5B as found by Kimber and Riley (1963) for nulli-5B haploids. A quadrivalent association was observed in one cell. The trivalent configurations were chain or Y types. Many univalents exhibited end-to-end associations (Riley and Chapman 1957) in which chiasma formation was not involved. In one instance three chromosomes were involved in this type of association. Side-by-side associations, in some cases with end-to-end associations in the same cell, were also common. Almost certainly the bivalent and multivalent configurations comprised or incorporated the two homologous 5D chromosomes.

Due to the absence of chromosome 5B, pairing in a nulli-5B di-5D haploid is obviously greater than that reported for euhaploids and, as expected, approaches that for nulli-5B haploids. Due to the presence of the two 5D homologues, pairing per cell

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would be expected to be more intense in the haploid studied than in nulli-5B haploids. Accurate statistical comparisons for pairing between the two situations are difficult in the absence of standard errors for the appropriate means. If the obvious effect of 5D chromosomes in the nulli-5B di-5D haploid is removed by considering them in the bivalent or multivalent configurations,  $8 \cdot 01$  of the remaining 19 chromosomes remain as univalents. In the nulli-5B haploids reported by Kimber and Riley in the 20 non-homologous chromosomes  $7 \cdot 83$  remained unpaired. The percentages of univalents among non-homologous chromosomes ( $42 \cdot 2$  and  $39 \cdot 2$  respectively) are comparable. Excluding homology between 5D chromosomes,  $57 \cdot 8\%$  of chromosomes were involved in bivalent and multivalent configurations in the nulli-5B di-5D haploid whilst  $60 \cdot 8\%$  were involved in the nulli-5B haploids reported.

The interaction of temperature and chromosome associations was not studied since the effect of temperature on synapsis and chiasmata frequencies previously cited was published subsequent to the current investigation. The nulli-5B di-5D plant was grown in the open, the temperature range during meiosis being approximately  $12 \cdot 0 - 23 \cdot 5^{\circ}$ C. Riley *et al.* (1966) found that chromosome 5D showed no dosage effect for mean chiasmata frequency per chromosome at the diploid level. If dosage effect is shown in haploid plants with two 5D chromosomes, presumably it would be most evident at constant low temperatures when 5D control of synapsis operates. In this investigation two doses of chromosome 5D caused little alteration to the degree of homoeologous pairing previously reported for nulli-5B haploids.

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