The Analysis of Chromosome Pairing in *Triticum* Hybrids

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IN a series of studies of *Triticum* hybrids Kihara and his associates have made two important advances. They have shown, first, the degree of pairing of the chromosomes, and, secondly, the manner of its variation, more exactly than such phenomena have been shown before in hybrids. They have achieved both these results by the individual recording and statistical analysis of extensive observations.

They have, however, recorded only one degree of variation in pairing; the chromosomes either pair or do not pair (trivalent combination being, of course, the result of pairing of two chromosomes with a third). It is recognised that variations occur in what is called the “strength” or “closeness” of the pairing, but such variations have not been treated statistically.

Now where pairing is complete in the parents and incomplete (and variable) in the hybrids an exact record of its variation is no doubt a sufficient indication of the conditions of pairing in a particular hybrid. But for comparative purposes it is necessary to have some record of the “strength” of pairing in the hybrids and of its “strength” in the parental species (if this varies). This is particularly true where (as in many cases) pairing in the hybrids is complete just as it is in the parents.

For this purpose it is necessary to understand the structure of the bivalent chromosomes and describe it in understood terms. Such a method I have described elsewhere (1931 a). It rests on the view that chromosomes are united from diplotene to metaphase of the first division by chiasmata which are exchanges of partner amongst the four chromatids of the bivalent. Where the chromosomes are united terminally it is assumed that this association has arisen from the
terminalisation of chiasmata originally formed interstitially. Since in
pure forms the frequency of these chiasmata at diplotene (and in the
absence of terminalisation, at metaphase) is proportional to the length
of chromosomes paired at pachytene, the number of chiasmata is a
fairly good index of the homology (or more precisely, similarity of
structure) of the paired chromosomes. I have shown several kinds of
evidence for believing that this interpretation of chromosome be-
behaviour is universally valid, (with the exception of particular chromo-
somes in certain animals, particularly hemiptera).

Where a certain amount of terminalisation occurs, as is evidently
the case in Triticum, a record of chiasma frequency at metaphase is a
less direct indication of homology, because the higher chiasma fre-
quencies are reduced. Nevertheless it is the most accurate available,
since the earlier stages cannot be accurately observed in this genus.

There is at present no record or illustration of chiasma frequency
and bivalent form in any species of cereal, in spite of the extensive
studies of hybrids (cf. Watkins 1930). I have therefore examined
these for the purpose of more exact comparison with corresponding behaviour in hybrids. For this study Mr. A. E. Watkins has kindly lent me smear preparations that he has made from his own material growing at Cambridge. I arrive at the following conclusions:

(i) The number of chiasmata in the bivalents of the *species* varies from one to three. According to their number and distribution rod- and ring-shaped bivalents are formed. Rod-shaped bivalents have

Figs. 4–7. The bivalent chromosomes of *T. turgidum*, *T. dicoccum* and their *F₁* hybrid (n=14). Fig. 4, aceto-carmine, ×2200; Figs. 5–7, Flemming-gentian violet, ×3200.
usually been regarded as a sign of "weak" affinity. It is therefore important to recognise that (as in most organisms) they may be formed from the pairing of identical chromosomes.

(ii) The number of terminal chiasmata is none, one or two in each bivalent.

(iii) Terminalisation is incomplete and (therefore) variable in its effect, the terminalisation coefficient (proportion of total chiasmata that are terminal) in different metaphases varying from 0.4 to 0.8.

(iv) The chiasma frequency in the hybrid between *Triticum turgidum* and *T. dicoccum* is lower than in the two parents, so that there are more rod-shaped bivalents in the hybrid (the number being variable of course in all three.)

(v) Pairing is nevertheless usually complete in the hybrid. Occasional quadrivalents or trivalents and univalents are formed. This shows that pairing may take place between chromosomes derived from the same parent in crosses between tetraploid *Triticum* species, as genetical evidence indicates (DARLINGTON 1927).

**Notes.** (a) The proportion in bulk of the chromosomes fixed by medium FLEMMING and those fixed by aceto-carmine (MCCLINTOCK'S method) is approximately as 1 to 4. Such a difference may be found to follow the use of the same fixative in mass-fixations, owing to differences in penetration; but is characteristic of the fixative in smear preparations.

(b) Figure 4 shows proximal interlocking of two bivalents; figure 2 shows "proximal-distal" interlocking. This type of observation has been discussed elsewhere (GAIRDNER and DARLINGTON 1931).

**Conclusion**

1. A study of chiasma frequency in *Triticum* species and hybrids shows variation in both but a relative reduction in the hybrids. This difference in affinity cannot be accurately recorded by other means.

2. Formation of two bivalents in a tetraploid, instead of a quadrivalent, is an unknown measure of the relative similarity of the four chromosomes concerned. Probably, in organisms with polarisation of the nucleus at zygotene, changes of partner amongst four homologous chromosomes are less frequent than in the absence of polarisation, owing to association beginning regularly at the ends. The fact which I pointed out earlier (1930) that in *Triticum-Aegilops* hybrids the pairs are so largely terminally associated (i.e. have a higher degree of terminalisation) is perhaps a symptom of the reduced amount of pachytene
pairing in the middle regions. This would follow in the hybrids if there were polarisation, for chromosomes would begin pairing at the ends and any change in homology (owing to the linear sequence of the pairing chromosomes being different) would interrupt pairing in the middles (cf. Dobzhansky 1931, Darlington 1931b, Appendix 5). Probably, therefore, quadrivalents are formed less frequently in Triticum hybrids than they would be with random association as in Hyacinthus.

3. The type of analysis suggested here gives a more direct indication of the length of chromosome paired at pachytene than any other, but it must be borne in mind that this pairing is conditioned not only by similarity of materials but by similarity of their arrangement. Differences of arrangement are important in preventing the pairing of chromosomes, but less important presumably in differentiating species physiologically.

Thus (i) comparative chiasma frequency of parents and hybrids, (ii) the occurrence of differential affinity amongst the homologous chromosomes in a polyploid and its possible modification by polarisation and (iii) the possible lack of correlation between structural and non-structural changes in the chromosomes, must be taken into consideration in arguing relationship of chromosomes from their behaviour in hybrids.

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References


