A STUDY OF PACHYTENE CHROMOSOME PAIRING IN A CORN-TRIPSACUM HYBRID DERIVATIVE¹

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THE concept of chromosome homology is not a precise one. When pressed for a definition, we may say that cytologically, homologous chromosome regions are those which seem by and large to match and are found synapsed at pachytene, but we must immediately amend this by saying that under some conditions non-homologous chromosome regions are also found closely paired at pachytene (McCLINTOCK 1933). These latter regions are considered non-homologous because we know that pairing partners which match each more closely exist elsewhere. The pairing of these non-homologous regions is thought to be a haphazard satisfaction of a generalized tendency of single parts to pair, but may be indistinguishable, even when chromomere patterns are compared, from the pairing of homologous regions. It is also true that under certain conditions chromosome regions which are homologous are sometimes found not to be paired at pachytene. It is not clear whether such pachytene pairing failure is due to synaptic failure or to precocious opening of synapsed chromosomes, but it is found in a variety of plants each homozygous for a type of recessive gene usually called "asynaptic" and, perhaps generally, in slightly unbalanced complements (MORGAN 1956; MAGUIRE 1960). Thus pachytene pairing of homologous chromosome regions is subject to genetic and environmental interference. Crossing over occurs regularly at meiosis (with an impressive list of exceptions) between homologous chromosome regions.

It is implicit in cytogenetic theory that homologous chromosome regions carry identical loci. At any locus several allelic forms may be possible, but chromosome pairs which differ only in that they are heterozygous at one or more of their loci are considered homologous throughout their length. Since pachytene pairing appears to be locally specific in structural hybrids, the extrapolation is commonly made that homologous genes are the specific units of pairing affinity, with the gross chromosome pairing observed as a composite effect of many small parts. It seems probable that if specific pairing affinities exist on the level of individual genes, that these affinities vary in strength from one locus to another and between different alleles at a given locus, as well as with factors external to these genes. To the writer's knowledge no direct evidence is available on the question of whether heterozygous genes have as strong an affinity for each other as homozygous ones, although this question might be amenable to experimentation. It should be borne

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in mind that the term "heterozygous" covers gene pairs which may differ only slightly in effect, and presumably in constitution, and also gene pairs which differ widely in effect, and differ to an unknown, but probably (some of the time at least) to a much greater extent, in constitution. Such genes are called alleles because they seem to occupy the same position. Initially identical loci theoretically may come to differ in divergent groups with the accumulation of differences in interaction, or with changes in details of chromosome structure, until their common origin is no longer genetically detectable. During the divergent process similar chromosome regions seem to lose their facility for crossing over and their specific pairing affinity. Synapsis is sometimes imperfect (although no structural differences between the two chromosome sets are apparent) in hybrids between different strains of a species as well as in interspecific hybrids.

Thus, although the generalization is convenient that homologous chromosomes are paired at pachytene and carry the same kinds of genes in the same order, we may expect in practice to find many cases of similar chromosome regions which cannot be so neatly categorized. In separate species a locus may have the same alleles, alleles which differ only in degree of effect, or alleles which differ more widely in effect (FABERGÉ 1944). As shown in the present paper and elsewhere, in interspecific hybrids and their progeny chromosomes or chromosome segments may synapse regularly, or regularly only when a closer homologue is not available, or only so often as segments considered non-homologous usually pair. This paper describes work on corn backcross progenies of corn-Tripsacum hybrids. References to chromosome homology are made with the realization that the concept is a relative one.

MATERIALS AND METHODS

The plant material studied was a 21 chromosome stock containing a pair of *Zea-Tripsacum* interchange chromosomes as illustrated in Figure 1. The interchange occurred in an early corn backcross generation of a *Zea-Tripsacum* hybrid and involved a distal portion of the short arm of corn chromosome 2 and a distal portion of the long arm of a *Tripsacum* chromosome which was itself about half as long as corn chromosome 2. The segment from the *Tripsacum* chromosome, now located in the short arm of chromosome 2, carried a terminal knob and at least two loci normally present in the region of corn chromosome 2 for which it had been exchanged. The segment of the *Tripsacum* chromosome containing its centromere, now attached to the distal segment from corn chromosome 2, showed no apparent homology to any corn chromosome region.

In 20 chromosome plants heterozygous for the exchange, the interchange chromosome 2 was usually found paired at pachytene with the normal corn chromosome 2 in a perfectly regular fashion so that, except for the presence of the terminal knob, the bivalent could not be distinguished from one comprised of two normal corn chromosomes 2. Analyses of occasional pairing failures, as well as genetic recombination, which occurs only very rarely in this region, have been set forth elsewhere (MAGUIRE 1960).

FIGURE 1.—Diagrams showing composition of Zea-Tripsacum interchange chromosomes and the combinations in which they occur in knob (+) and knob (-) plants.

Twenty-one chromosome plants were of two types, those carrying both interchange chromosomes, which will be called knob (+) plants, and those carrying two normal corn chromosomes 2 and the interchange chromosome containing the apparently non-homologous portion of the Tripsacum chromosome attached to the distal segment of the short arm of corn chromosome 2 (Figure 1). The latter type, which will be called knob (-), contained this distal segment of the short arm of corn chromosome 2 in triplicate. Metaphase trivalent frequencies have been found usually to approximate 90 percent in knob (+) plants and 69 percent in knob (-) plants (MAGUIRE 1957). Trivalent configurations at pachytene were of the types illustrated in Figures 2 and 3. All plants were the progeny of seven 21 chromosome knob (+) plants pollinated by a chromosome 2 genetic tester stock.

This study was undertaken to analyze more fully the pairing behavior of the chromosomes described above and to estimate the physical length of the Tripsacum segment exchanged for a portion of corn chromosome 2 of equal length. This length is expected to be equal to that length of the interchange chromosome 2 which is not paired in trivalent configurations of knob (+) plants, and to the length of normal corn chromosome 2 which synapses with the extra chromosome in these configurations. In the analysis which follows the latter measurement was used for simplicity and to facilitate comparisons to pairing behavior in knob (-) plants. Inference from such measurements is complicated by the fact that in most trivalents all three chromosomes are found to be unpaired in a region (usually short) around their point of branching (the "b" region of Figure 3).

Microsporocyte samples were fixed immediately after collection in alcohol-acetic 3:1 mixture and refrigerated until microscopically examined in aceto-carmine smears. Camera lucida drawings were made (with uniform settings) of all analyzable trivalent configurations from all pachytene cells where chromosomes appeared flat and unstretched. All or nearly all available pachytene material was examined. Some bias may have been imposed on the data by the necessary selection for study of analyzable cells.

RESULTS

The mean of 170 measurements of the length of the extra chromosome at pachytene when involved in a trivalent configuration was 44.1 percent of the total length of corn chromosome 1. The fact that this figure did not differ significantly from the mean of 54 measurements of the extra chromosome as a univalent (44.3 percent of the total length of chromosome 1) supports the validity of comparisons between linear measurements of paired and unpaired chromosome regions.

A total of 115 measurements in 16 knob (+) plants and 54 measurements of five knob (−) plants were made of the percent of the total length of chromosome 2 which was found to be paired in trivalents with the extra chromosome (the "a" region of Figure 3). F tests of whether variances differed among samples from different knob (+) plants or among samples from different knob (−) plants indicated that they did not at the five percent level, and analysis of variance indicated that plant sample means did not differ among knob (+) plants or among knob (−) plants at the five percent level. Therefore, all data were pooled for knob (+) plants and compared to data pooled from knob (−) plants. The cumulative percent frequency distributions of this measurement in knob (+) and knob (−) plants (Figure 4) were tested for goodness of fit to normal distributions by chi-square tests with class intervals set so as to contain equal expected frequencies as suggested by TATE and CLELLAND (1957). The sample distributions were

FIGURE 2.—Photomicrographs of trivalent configurations. A.—Trivalent from a knob (+) plant with the segment of corn chromosome 2 (located in the extra chromosome) paired with the unaltered corn chromosome 2. The knob-bearing segment from the *Tripsacum* chromosome is unpaired. There is pairing failure in the region of branching of the trivalent. B.—Trivalent from a knob (−) plant with the distal region of the short arm of corn chromosome 2 (located in the extra chromosome) paired with one of the unaltered chromosomes 2. There is pairing failure in the region of branching of the trivalent. C.—Trivalent from a knob (−) plant with the extra chromosome paired with a corn chromosome 2 as in A and B above. In addition there is non-homologous pairing of the *Tripsacum* segment of the extra chromosome with the end of the other corn chromosome 2 for a short distance. There is pairing failure in the region of branching of the trivalent. D.—E.—Trivalents from knob (+) plants with the corn segment in the extra chromosome paired with the unaltered corn chromosome 2 as in A, B, and C above. In addition there is non-homologous pairing between the two *Tripsacum* segments. There is pairing failure in the region of branching of the trivalent. F.—Same as D and E but with pairing complete except for a short region near the terminal knob. All types of configuration occurred in all plants. Magnification is about 1000 $\times$.

FIGURE 3.—Semidiagrammatic interpretations of the photomicrographs of Figure 2. Various regions are labelled as follows: a.—pairing of distal segments of corn chromosome 2, one located in an unaltered chromosome, the other attached to a Tripsacum segment in the extra chromosome. b.—region of pairing failure. c.—non-homologous pairing: of two Tripsacum segments in trivalents of knob (+) plants, or of the Tripsacum segment in the extra chromosome with corn chromosome 2 in trivalents of knob (—) plants. d.—pairing of unaltered portions of corn chromosome 2 in trivalents. Centromeres, where recognizable, are indicated by crossbars.

found not to differ from normal distributions at the five percent level (or even at the ten percent level). In an F test the variance of all measurements from knob (+) plants (70) did not differ significantly from the variance of all measurements of knob (-) plants (68) at the ten percent level. The means of these measurements, however, were found to differ at the one percent level in a t test. The mean for knob (+) plants was 20.2 percent with a five percent confidence interval estimate of 18.9 percent to 21.5 percent, and for knob (-) plants the mean was 14.6 percent with a five percent confidence interval of 12.7 percent to 16.5 percent.

In most trivalents in the region of branching all three chromosomes were found

FIGURE 4.—Cumulative percent frequency plots on normal probability scale of observed distributions of the percent total length of chromosome 2 paired with the extra chromosome in trivalent configurations of knob (+) and knob (-) plants. Plots expected for normal distributions with the means and variances observed are also shown.

to be unpaired for a short distance (the "b" region of Figure 3). In the 115 trivalents from knob (+) plants the average of this distance was 8.5 percent of the total length of chromosome 2 with the median at seven percent, and in the 54 trivalents from knob (-) plants the average of this distance was 8.2 percent of the total length of chromosome 2 with a median again at seven percent. A chi-square test of the goodness of fit of these cumulative percent frequency distributions (with class intervals again set so as to contain equal expected frequencies) indicated that they differed significantly from normal distributions at the one percent level. These cumulative frequency distributions of knob (+) and (-) plants were, however, very similar as illustrated in Figure 5. They were characterized by larger frequencies at smaller extents. By a KOLMOGOROV-SMIRNOV test the knob (+) and knob (-) samples did not differ significantly at the 20 percent level. Since knob (+) and knob (-) plants did not seem to differ, it appears that the extent of this region of pairing failure was probably not related to the presence of the knob-bearing *Tripsacum* segment. A rank difference test of correlation of the average length in microns of chromosome 2 in each plant to the average percent of its length unpaired gave an r_d (rank difference correlation coefficient) of -0.57 which is significant at the one percent level (Figure 6). Such absolute measurements of total length are probably influenced by the amount of pressure applied in making the squash preparations, but in a general way presumably reflect the relative stages of advancement of the cells, with more advanced cells showing shorter lengths. It appears then, that this pairing failure increases somewhat with stage advancement and may represent an opening, probably in both directions, after initial pairing, rather than a failure to synapse.

FIGURE 5.—Cumulative percent frequency polygons of the percent of the total length of chromosome 2 found to be unpaired in trivalent configurations from knob (+) and knob (-) plants.

FIGURE 6.—Percent total length chromosome 2 found to be unpaired in trivalent configurations as a function of the average total length of chromosome 2. Each point represents the average values for a plant, and the number beside it is the number of observations which were averaged to give this value.

The average extent of this region of pairing failure must be considered in the estimation of the length of the exchanged chromosome segments. If it is assumed that an opening occurs and proceeds at an equal rate in both directions, an estimation of the length of chromosome 2 which has been replaced by the *Tripsacum* segment is given by adding half the average extent of percent of chromosome 2 where pairing failure occurred (about 4.2 percent), to the average percent of chromosome 2 found paired with the extra chromosome (20.2 percent) in trivalents of knob (+) plants. This total is 24.4 percent of the total length of chromosome 2. In 19 of the 115 trivalents of knob (+) plants there was virtually no pairing failure. The average extent of pairing of the extra chromosome with the normal chromosome 2 in these trivalents was about 26 percent. This may be considered a direct estimation of the length of segments exchanged, and although it is based on a small number of measurements, it is in fair agreement with the estimate made above. It seems probable that the extent of chromosome 2 replaced by a similar segment from *Tripsacum* (of the same length) was about 24 to 25 percent of its total length. It cannot be concluded, however, whether or not the *Tripsacum* chromosome from which the knob-bearing segment was derived con-

tained this region as a segment from previous corn admixture. So far there has been no adequate test of whether the remainder of the *Tripsacum* chromosome also bears partial homology to part (or parts) of corn chromosome 2. Since early backcross generations where pachytene analysis was not possible, this region has been present only in 21 chromosome plants where it is attached to the distal segment from the short arm of corn chromosome 2. Under these conditions preferential pairing of the sort which discriminates against the pairing of the knob-bearing segment with the corresponding segment of corn chromosome 2 in trivalents, would also prevent the pairing of this region. The exchange which produced the interchange chromosomes described here may have been a crossover type of event.

As indicated in Figures 2 and 3, pairing occurred in some trivalents of knob (+) plants in such a way that the segment of the *Tripsacum* chromosome transferred to corn chromosome 2 appeared synapsed with the remainder of the *Tripsacum* chromosome (the "c" region of Figure 3 D, E and F). Unless the chromosome derived from *Tripsacum* prior to exchange with corn chromosome 2 was an isochromosome with two like regions arranged in reverse order, this pairing is probably non-homologous. Since the centromere of this chromosome was not centrally located (the chromosome's arm ratio was about 3.3:1), it seems unlikely that it was an isochromosome. As shown in Figure 2 and 3, pairing also occurred in trivalents of knob (−) plants between a normal corn chromosome 2 and the *Tripsacum* segment of the extra chromosome (the "c" region of Figure 3 C). This pairing is also probably non-homologous. The pairing of these regions in knob (+) and knob (−) plants was comparatively irregular. It occurred in 169 of 469 knob (+) sporocytes (about 36 percent) and in 15 of 89 knob (−) sporocytes (about 17 percent). In both cases samples of frequency of occurrence from different plants ranged from zero percent to over 70 percent. Since the difference between knob (+) and knob (−) sporocytes was significant at the one percent level by a chi-square test, there seems to have been a stronger affinity (when there was no other chance for pairing) between two *Tripsacum* segments than between a corn and a *Tripsacum* segment, although all these regions were probably non-homologous in the usual sense. Since the variabilities within both knob (+) and knob (−) samples were great, other factors must have been important in determining whether or not this non-homologous pairing occurred.

The extra chromosome was found folded back and paired with itself near its center in seven of the 54 univalents found (about 13 percent). This pairing is similar to the non-homologous pairing which occurred in trivalents of knob (−) plants described above (the "c" region of Figure 3 C). It involves pairing of the centromere carrying *Tripsacum* segment and distal region from corn chromosome 2.

As reported earlier (MAGUIRE 1957), knob (+) plants usually show a metaphase trivalent frequency of about 90 percent, while knob (−) plants usually show a trivalent frequency of about 69 percent. Heretofore, although almost all metaphase cells could be classified easily as to whether the extra chromosome was involved in a trivalent configuration, only small proportions of pachytene cells

have been classifiable, and there was doubt whether the differences regularly noted between knob (+) and knob (−) plants in metaphase trivalent frequency were due to differences in frequency of trivalent formation at synapsis or to differences in frequency of chiasma formation (MAGUIRE 1957). Some information is now available on this question. In a knob (−) plant it was possible to classify 205 pachytene cells of a total of 563; of these 133, or 65 percent, contained a trivalent. Sixty-one percent of metaphase I cells from this plant showed a trivalent configuration. In a knob (+) plant it was possible to classify 60 pachytene cells of a total of 135; 59 of them or 98 percent showed a trivalent, while 98 percent of metaphase I cells showed a trivalent. This evidence supports the view that chiasma formation usually follows synapsis and that metaphase trivalent frequency gives a fair estimate of trivalent formation at synapsis.

DISCUSSION

It is of interest that the average percent of normal chromosome 2 paired with the extra chromosome in knob (−) plants was significantly less than that in knob (+) plants. The two normal chromosomes 2 in knob (−) plants probably synapse in the region present only in duplicate (the "d" region of Figure 2) in such a way that their pairing on the average extends into the region where three homologous segments are present, before the extra chromosome can pair with one of them for the entire region for which it, too, is homologous. It seems unlikely that the extra chromosome of knob (−) plants consistently differed from that of knob (+) plants since all were siblings of 21 chromosome knob (+) female parents. The normal corn chromosomes 2 of both knob (+) and knob (−) plants were derived from the same genetic tester pollen parents, and it is unlikely that they were structurally altered in knob (−) plants. The behavior could be explained by assuming that pairing is initiated between the two normal corn chromosomes of knob (−) plants somewhere near the usual branching point of trivalents (and perhaps at a number of other points also) at about the same time one of them pairs with the extra chromosome more distally, and then proceeds in both directions at about the same rate. It is also possible that pairing is usually initiated earlier in the region where only two homologs are present, or that it proceeds faster here. It is impossible to choose among the possibilities with the information available. Since trivalents in these knob (−) plants are formed only with a frequency of about 69 percent, about one third of the time the extra chromosome is completely left out as a univalent. This would be expected if a zipper-like closing occurs once contact has been established, and the assumption is made that odds are equal that any two of the three chromosomes will establish contact in the region where all three are homologous.

It is also of interest that the variances of the percent of normal chromosome 2 paired with the extra chromosome in trivalents did not differ significantly at the five percent level in knob (+) and knob (−) samples. A large and similar part of the variation in the two samples was caused by variation in the extent of pairing failure in the region of branching of trivalents. The residual variation must also

be supposed to be similar in knob (+) and knob (−) plants. In knob (+) plants this residual variation would probably be due to differential shortening of various chromosome regions (real and/or artifact of measurement) and conceivably to occasional partial pairing of the corresponding corn and *Tripsacum* segments. Differential shortening, if it occurs, would probably be equally present in knob (−) plants. Whatever the factors are which influence the extent of pairing with the extra chromosome in knob (−) plants, this distance seems to be about as rigidly determined here as in knob (+) plants where preferential pairing presumably sets this length. Since three homologous segments were present in knob (−) plants, a continuous series of configurations would be expected ranging from trivalents with about 75 to 76 percent of the two normal chromosomes 2 paired with each other, up to nearly 100 percent of these paired. The results do not conform to this expectation but are consistent rather with the interpretation that synapsis is initiated at rather precise positions, or that its course is somehow directed toward a predetermined end no matter how it begins. It is not unreasonable to suppose that different regions of a chromosome may differ in their affinity for the homologue, and that those parts with the strongest tendency to pair would usually do so first. Such regions might or might not be equivalent to the "conjunctive segments" postulated by COOPER (1944) to describe chromosome configurations in meiotic prophase, and metaphase of *Olfersia*.

A satisfactory explanation of the mechanism of synapsis must take into account preferential pairing of the sort demonstrated by the material described here. In plants where closest homologues are corn and *Tripsacum* segments, these have been found to pair with a frequency of about 93 percent (MAGUIRE 1960). Two corn segments have been found to pair with a frequency of about 90 percent, however, when the corresponding *Tripsacum* segment is also available. Two non-homologous *Tripsacum* segments seem to pair more often (frequency about 36 percent), when no other pairing partner is available, than do corn and *Tripsacum* non-homologous segments when faced with the same situation (frequency about 17 percent). If pairing is initiated by chance contact of moving chromosomes, as suggested by DELBRUCK (1941), provision must be made for release of relatively non-homologous members (if these should be first to meet) in favor of more closely matched pairs at a later collision. If on the other hand the initiation of synapsis results from specific long range forces of attraction between likes, there must be a hierarchy of degrees of attraction to correspond to the hierarchy of degrees of likeness of chromosome regions. Where three similar parts are present and initially separated in the nucleus, progress toward the meeting of any two could be impeded by the presence of the third.

The mechanical problems of synapsis of greatly extended chromosomes are so great that the suggestion of SMITH (1942a,b), that pairing is generally initiated in the premeiotic anaphase or telophase when chromosomes are more condensed, seems to deserve more consideration than it has received. A number of authors in many groups (reviewed by SMITH) have presented evidence for association of homologues at or by telophase of the last premeiotic division. WILSON (1912) suggested earlier that such premeiotic pairing might occur generally. If a juxta-

position of homologous chromosome regions is achieved at this time, more intimate pairing could be accomplished as the chromosomes uncoil. Such leptotene and zygotene configurations as have been figured would not be at variance with this interpretation when it is recognized that incomplete pairing of chromosomes at early meiotic prophase may represent failure of synapsis or its precocious opening (MAGUIRE 1960). Initial pairing of chromosomes in a condensed state would help to explain why interlocked bivalents occur so rarely at pachytene. In the writer's experience of thousands of corn microsporocytes at pachytene, no convincing case of such interlocking has been seen. In *Neurospora* where karyogamy immediately precedes meiosis, homologous chromosomes come together in a state at least as condensed as at metaphase and proceed to pair more intimately as they lose their condensation (SINGLETON 1953). Initial pairing of heterochromatic portions in *Edessa* (SCHRADER 1941) might be interpreted as the coming together of the more condensed regions of homologues. Boss (1954) described chromosome pairing in somatic anaphase of newts.

If condensation facilitates efficient movement of homologous chromosomes toward each other, it is not, of course, to be inferred that chromosomes must pair each time they are condensed. It must be supposed that other causally related special conditions pertain at times when such pairing occurs. The intimate pairing of synapsis might occur only when a loss of condensation immediately follows the juxtaposition of condensed chromosome pairs. If synapsis actually occurs earlier than has been generally supposed, it may precede chromosome reduplication. Under these conditions the hypotheses which require that crossing over occurs during reduplication become more plausible.

SUMMARY

1. Pachytene trivalent configurations were analyzed in 21 chromosome plants of two types. In one type two reciprocal interchange chromosomes were present, one comprised of a corn chromosome 2 with a terminal knob-bearing segment from *Tripsacum* in the distal region of its short arm, the other a *Tripsacum* chromosome with the distal region of corn chromosome 2 in its long arm. These are called knob (+) plants. In the other type of 21 chromosome plant, two normal corn chromosomes 2 were present, and the extra chromosome was the *Tripsacum* chromosome described above with distal region of the short arm of chromosome 2 in its long arm. These are called knob (−) plants.

2. The lengths in the interchange chromosomes of segments exchanged were equal and are estimated to be about 24 to 25 percent of the total length of corn chromosome 2.

3. At the point of partner exchange most trivalents contained a region, usually short, where all chromosomes were unpaired. There was a negative correlation (significant at the one percent level) of the extent of this region with the absolute length of corn chromosome 2. This suggests that the trivalents may have been progressively opening in this region as pachytene advanced.

4. The percent of chromosome 2 which was paired with the extra chromosome

in trivalents was significantly greater in knob (+) plants than in knob (−) plants where the distal segment of corn chromosome 2 was present in triplicate. The variances of this measurement in knob (+) and knob (−) plants did not differ significantly.

5. Theoretical implications are discussed.

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