Chromosome Pairing in Intercrosses Between Stocks of Interchanges Involving the Same Two Chromosomes in Maize

II. Pachytene configuration in relation to breakage positions¹

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The first paper of this series (Tabata 1962) is a report of the relationship between the diakinesis configurations and differences in break positions in crosses between stocks of interchanges involving the same chromosomes.

This is a report of studies that utilize certain of the same intercrosses to provide information as to where on the chromosomes pairing is initiated, how it proceeds and what factors affect the resulting configurations at and later stages. Evidence is obtained by studying the effect of changes in the relative positions and lengths of interchanged and non-interchanged segments on the configurations observed at pachytene.

Materials and methods

The 2-6 interchange stocks used in the present study are the same as those described in the first paper of this series (Tabata 1962). Anthers of F₁ plants were fixed in a fresh mixture of 3 parts 95% ethanol and 1 part glacial acetic acid, and kept in 70% ethanol in a freezing chamber at about 10~15°F. Microsporocytes were smeared on the slide in a small drop of propiono-carmin. Artificial pressure other than from the weight of cover glass was not applied on the specimen to avoid stretching, dislocation, and extreme flattening of the delicate pachytene chromosomes. The preparation was then gently heated over a flame from a spirit lamp. Most of the observations were made using temporary slides.

The stocks used commonly possessed the large knob situated in the long arm of chromosome 2, and the two small knobs in the long arm of chromosome 6.

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Chromosome 6 is attached to the nucleolus by a deeply staining nucleolar organizing region, and a small knob terminates the satellite.

Results

The results obtained from the various intercross combinations will be presented in groups according to the types to which they belong.

Type 1a intercrosses

In type 1a intercrosses, the break points in the two stocks crossed are in opposite arms on both interchanged chromosomes. The break points in the parental stocks and the constitution of the chromosomes in the intercross F_1 are illustrated in Fig. 1, for the $T2-6a \times T2-6b$ intercross. The regions on the arms are designated by numbers.

The results from two type 1a intercrosses, $2-6a \times 2-6b$ and $2-6a \times 2-6(6049)$, will be presented together as they showed similar cytological behavior. In $2-6a \times 2-6b$, the "between breaks" segment in chromosome 2 (*i.e.*, regions 2 and 3) comprises about 50% of the total length of chromosome 2, and that in chromosome 6 (*i.e.*, regions 6 and 7) includes 43 to 49% of the total length of chromosome 6. Hence the total length of interchanged segments is about the same as that of "between-breaks" segments. In $2-6a \times 2-6(6049)$, the arrangement of break points is similar except for the break position in the long arm of chromosome 6, which makes the interstitial segment 7 on 6L half as long as that in $2-6a \times 2-6b$ and region 8 that much longer. Here the "between-breaks" segments constitute about 43% of the total length of the two chromosomes.

At the diakinetik stage of $a \times b$, the four interchanged chromosomes formed two separate "pairs" in 76% of the spore-mother-cells, and an association of four in 24% of the cells. In $a \times 6049$, the corresponding figures are 56% and 44% (Photos. A and B). Metaphase cells also showed 10 pairs or a complex of four plus 8 pairs. The arrangement of these chromosomes at metaphase I and their disjunction at anaphase I were apparently normal.

Considerable numbers of pachytene cells showed two separate "pairs".

Fig. 1. $2-6a \times 2-6b$ (type 1a); Top: diagram of chromosomes 2 and 6. Arrows indicate the approximate breakage positions in $2-6a$ and $2-6b$ interchanges, the regions of the chromosomes being designated by numbers. Middle: diagram of the four interchanged chromosomes in the F_1 plant. Bottom: diagram illustrating the pachytene configuration expected from complete synapsis of the four interchanged chromosomes in the F_1 .

Photos. A-G. All the photomicrographs are at the same magnification. $\times 1050$. Arrows in the photographs point to the centromere regions both in paired and unpaired conditions. A, a ring of four chromosomes at diakinesis in an F_1 plant of the intercross 2-6a $\times$ 2-6(6049). B, diakinesis from the same plant as Photo. A. An unequal "pair" from the association of two interchanged chromosomes, 2^{6a} (longer member) and 6²(6049). C, photomicrograph of the pachytene configurations shown in Fig. 2. D, photomicrograph of the configuration shown in Fig. 4. E, photomicrograph of the configuration drawn in Fig. 8. F, pachytene association of four interchanged chromosomes in an F_1 plant of the intercross 2-6b $\times$ 2-6c. The distal parts of all the chromosomes are associated. 6L is identified by a small but conspicuous knob. 2L extends vertically in the center. The distal portion of 2S crossing above 2L, terminates on the periphery of the nucleolus. The long inverted segment of chromosome 2 failed to associate with its partner, both lying as single threads as seen in the central part of the configuration. G, photomicrograph of the pachytene configuration shown in Fig. 18.

The association in these was found to be always between homologous end segments. Only in rare figures were the ends of these "pairs" not associated. "Pairs" were never formed by the association of homologous centromeres in the intercalary segments. One member of each "pair" was longer than the other member. In spite of the difference in the total length between the members of a "pair", the homologous regions in or near both ends of the chromosomes were always paired. Each "pair" usually showed an intercalary loop often including a single centromere: Fig. 2 (Photo. C). In every one of these "pairs" there was an association of non-homologous parts in the intercalary segment. The loop tended to associate non-homologously with itself in many figures, often at two points as shown in Fig 3. An open loop was rather rare. The positions of the loops in "pairs" seemed to show some variation, also their relative sizes varied in different cells and within the same cells. Furthermore, the "pairs" attached to the nucleolus occasionally took unusual configurations in which no loop (Fig. 4, Photo. D) or a very small loop was formed, owing to non-proportional stretching or contraction of the members of the "pair". Another exceptional configuration is shown in Fig. 5. The shorter member associated with the longer

Figs. 2-5. 2-6a $\times$ 2-6(6049) (type 1a); Camera lucida drawings of the interchanged chromosome "pairs" at pachytene. 2, two "pairs" resulting from association between the interchanged chromosomes having homologous ends. The longer member of each "pair" shows a fold including a centromere. The non-homologous intercalary segments are intimately associated (see Photo. C). 3, two sets of folds have occurred in the intercalary segment of each "pair". 4, unusual configuration of the 2^aa/6²(6049) "pair" in which no loop was formed (see Photo. D). 5, another exceptional "pair", in which the end of the longer chromosome, 2^aa, did not pair with the homologous part in the shorter chromosome. Note the occurrence of foldbacks in this unassociated segment. $\times 1160$.

one along the entire length and the ends failed to pair. Initiation of folding-back was seen at two places in the unpaired segment of the longer member.

The above observations indicate that in these crosses chromosome ends played a major role in initiating chromosome association. The association initiated at the ends tended to move toward the inner region in spite of non-homology, unless it was prevented by a counter association independently initiated at a point in the inner region. It seems that a fold often occurred near or at the centromere region. The early occurrence of extensive non-homologous association in the inner segment seemingly eliminated the possibility of its association with the homologous part in the other "pair".

Only occasionally was there a configuration in which four arms radiated out from paired mid-regions of chromosomes as diagrammed in Fig. 1. One of these is shown in Fig. 6.

In the configurations with a complex of four at pachytene, the ends of the chromosomes always showed complete homologous pairing, except for the short terminal segment of 2S (region 1) which in some cells of a $\times 6049$ failed to associate. Intercalary regions were only partially synapsed, were unpaired, or associated non-homologously. As to specific intercalary regions, more extensive homologous pairing was observed in region 2 than in region 3, which nearly always showed extensive non-homologous association with regions 6 and 7 in the other chromosomes. Non-homologous association is shown in Fig. 6 between the distal portion of region 2 and a portion of region 7 on the other chromosome. In Fig. 7, large portions of the non-homologous interstitial segments 3 and 7 are associated in two of the arms. The complex of four in Fig. 8 (Photo. E) shows perfect pairing in the distal regions 1, 4, 5, and 8, but failure in region 3, part of which is associated non-homologously with region 7. As a consequence, only a partial loop was formed by region 2. Accordingly, the two "pairs" were brought together into a complex of four by synapsis in the proximal part of region 2. This type of configuration indicates that even in an association of four chromosomes, the intercalary regions were at a disadvantage in pairing. Also, the centromeres did not play any significant role in pairing in these figures, as the lack of correspondence in positions of homologous centromeres shows.

Configurations in which region 1 failed to pair are illustrated in Figs. 9 and 10. The failure of pairing in region 1 was correlated with complete pairing in region 2, indicating that the initiation of pairing was not in the end segment but in the intercalary region 2. Thus, the attraction force operating between homologues in region 2 competed with that between the homologous end segments (region 1), frequently overcoming the latter. However, such prevention of association in other distal regions was not observed, and the progression of association from them towards the intercalary regions forced the entire region of 7 and a part of region 3 into non-homologous association.

Figs. 6-10. Pachytene configurations resulting from the association of four interchanged chromosomes. 6 and 7, 2-6a $\times$ 2-6b (type 1a): Four arms radiate out from the mid-regions. Though all the ends are homologously associated, there are non-homologous associations between a part of intercalary regions 2 and 7 in figure 6 and between regions 3 and 7 in figure 7. 8-10, 2-6a $\times$ 2-6 (6049) (type 1a): 8, all the distal regions are homologously associated. Among the four interstitial segments, only segment 2 has associated homologously and in part, whereas non-homologous associations took place in the other three, 3, 6, and 7 (see Photo. E). 9, note that homologous associations took place in region 2 and in a part of region 3, whereas terminal regions 1 failed to pair. 10, note that the terminal region 1 of chromosome 6² (6049) did not pair with its homologous part but associated with region 3. On the other hand, region 2 as well as a part of region 3 have homologously paired with the corresponding homologous segments. $\times 1160$.

In an attempt to study crossing over in the four interchanged chromosomes, F_1 plants from the cross of $2-6a \times 2-6b$, heterozygous for gene markers, were crossed with pollen of the multiple recessive tester carrying no interchange. As to the physical locations of the markers used, *lg* is in the distal end of $2S$, within a region which includes only 4 chromomeres; *B* also is in the short arm, and *Pl* in $6L$, probably near the middle of the arm (McClintock 1931). Therefore, the locus of *lg* is undoubtedly in the region designated as 1 in Fig. 1, *B* supposedly in region 2, and *Pl* in region 7, probably fairly close to the break point.

The observed recombination between *lg* and *B* in the intercross F_1 was 32.4%, which is only slightly lower than the 34% for the standard map. This result agrees with the cytological observations that the pairing of homologous distal ends was usually complete both in "pairs" and in an association of four.

The occurrence of a single crossover in either region 3 or 6 (interstitial segments) could be detected by observing the frequently of spore quartets with only one spore with a diffuse nucleolus, referred to as a "one diffuse quartet type". Region 6 was very short, but region 3 included 40% of the length of $2L$. Nevertheless, single crossing over in regions 3 and 6, as

indicated by spore quartet counts, was only 1.2%. A very low value might be expected from the extensive non-homologous association noted in these regions at pachytene. Recombination between *lg* and *pl* was 30.9% in the progeny of one F_1 plant and 39.2% in another. It is probable that all or most of these crossovers were restricted to region 1 between *lg* and the break point in $2-6b$.

From both the genetic and cytological data, it appears highly probable that crossing over in the mid-regions of the complex of four is restricted almost entirely to the distal end of region 2 in $2S$ and that this association may bring about the change from "pairs" to an association of the four chromosomes.

$3 \times 6a \times 3-6b$. This intercross is of interest since it is the only one belonging to type 1a in which "pairs" were not the predominant configuration at diakinesis. All were associations of four chromosomes. In $3-6a$, both interchanged segments were short, as shown in Fig. 11. The one that included part of the satellite never associated with its

Fig. 11. $3-6a \times 3-6b$ (type 1a): Top: diagram of normal chromosomes 3 and 6, arrows indicating the breakage positions for two interchanges, $3-6a$ and $3-6b$. Center: diagram of four interchanged chromosomes in the F_1 plant from the intercross. Bottom: diagram of a pachytene configuration which might be expected from the association of these chromosomes in the F_1 plant.

homologue and the segment designated 1 from chromosome 3 was paired with its homologue only in part of the figures as *e.g.* Figs. 12 and 13. The failure of association in one end segment, namely the satellite, precluded the formation of "pairs". This appears to offer a clue to the explanation for differences in frequencies of associations of four chromosomes in the other two crosses in this group. One of the interchanged segments in the cross with the higher frequency was somewhat shorter than the interchanged segment from the same arm in the other cross, 2S. 8 vs. 2S. 69.

Spore quartet counts showed 68.1% were "no diffuse," 30.5% "two diffuse," and 1.4% "one diffuse." Since pollen abortion was 69.9%, the frequency of alternate : adjacent-1 : adjacent-2 segregation among the non-crossover quartets was calculated to be 30.1, 38.9, and 31.0. This approaches the 1 : 1 : 1 ratio expected from random segregation ; but the excess of adjacent-1 segregation is significant.

Type 1b intercrosses

In this type, the break points in one chromosome are on opposite arms, whereas those in the other chromosome are in the same arm. Pachytene analyses were made in the following four intercrosses : 2-6b $\times$ 2-6c, 2-6b $\times$ 2-6d, 2-6(6049) $\times$ 2-6c, and 2-6a $\times$ 2-6c. At the diakinetik stages of these intercrosses, all or nearly all of the cells showed a complex of four chromosomes plus 8 bivalents.

2-6b $\times$ 2-6c : As shown in Fig. 14, in this intercross, "between breaks" regions 2 and 3 comprised about 50% of the total length of chromosome

Figs. 12-13. 3-6a $\times$ 3-6b (type 1a): 12, pachytene configurations resulting from an almost complete synapsis of four chromosomes. Note that the short terminal segment translocated to the satellite region has succeeded to pair with its counterpart, though the satellites remained unassociated. 13, the cross-shaped configuration produced by homologous associations of the four chromosomes. In this case, the terminal segments of 3S are unassociated. $\times 1160$.

2 and the arrangement of homologous regions in the F_1 intercross is different from type 1a (compare with Fig. 1). The four chromosomes could form a ring by complete association of their homologous regions, but an inversion loop is necessary in the proximal regions 2 and 3. An inversion loop should be observed if pairing starts at the centromeres or in proximal regions as well as at the ends. None of the pachytene chromosomes showed such complete synapsis as illustrated in the diagram (Fig. 14). Though the distal regions were homologously associated, there was little or no synapsis in the intercalary regions. In Figs. 15 and 16 and Photo. F, the four chromosomes were associated only or mainly at their ends. In Fig. 15, however, a part of region 2 was forced to associate with a portion of non-homologous region 7 in the other chromosome owing to the probable progression of pairing from the distal end. In the configuration in Fig. 16 the two distal region 8's were associated only by their tip portions, the remainder showing foldbacks. This probably indicates that non-homologous association of region 2

Fig. 14. 2-6b $\times$ 2-6c (type 1b): Top: diagram of normal chromosomes 2 and 6, arrows indicating the break positions for the interchanges 2-6b and 2-6c. Center: diagram of the four interchanged chromosomes in the F_1 intercross. Bottom: diagram illustrating the pachytene configuration expected from the complete synapsis of the four chromosomes in F_1 .

with region 3 in the proximal parts of the chromosomes took place early enough to inhibit the progression of pairing that began at the tip of region 8.

In a few extreme cases, there was a cross configuration which superficially resembled that of a single interchange heterozygote (Fig. 17) but in which there was extensive non-homologous association in regions 2, 3, and 7. In this figure, the corresponding centromeres of 2 were at different positions. The absence of a loop appears to indicate that pairing had begun at the ends of the chromosomes and then proceeded in a zipper-like manner into the inner non-homologous regions. In occasional figures, contact had been made between homologues at some points in the intercalary segments before it was inhibited by the counteracting non-homologous association. For example, in Fig. 18 (Photo. G) region 2 was associated in the proximal portion including the centromere, while regions 3 and 7 were unpaired. When such homologous association occurred, it appeared to occur preferentially in region 2 over 3. Although region 2 was about 1.5 times longer than region 3, its relative location in the chromosome adjacent to the short terminal region 1,

Figs. 15-21. Camera lucida drawings of the pachytene association of the four interchanged chromosomes. 15-18, 2-6b $\times$ 2-6c (type 1b): 15, all the chromosome ends are homologously associated. The segments involving regions 2, 3 and 7 failed to form an inversion loop, instead showing non-homologous association or asynapsis. 16, non-homologous association has occurred in the inverted segments including the centromeres. Note that region 8 has paired by its tip, the rest forming foldbacks. 17, pachytene configuration produced by non-homologous association throughout the inverted segment. Note that the positions of centromeres of chromosome 2 do not correspond. 18, the configuration illustrating the homologous association in region 2 which terminates at the centromere. Regions 3 and 7 are unassociated (see Photo. G). 19-20, 2-6 (6049) $\times$ 2-6c (type 1b): 19, a large pericentric inversion loop resulted from homologous association in the segment. The ends of 2S are unassociated. 20, the pachytene configuration in which total non-homologous association took place in the inverted segment. The ends of 2S are unassociated in this case also. 21, 2-6a $\times$ 2-6c: the pachytene association of the four interchanged chromosomes. Note the darkly stained area near the center of "cross" where non-homologous association occurred. $\times 1160$.

seems to be the main reason for this preferential behavior.

Similar cytological results were obtained in the F_1 of $2-6b \times 2-6d$. The break positions in this cross were very similar except that the interstitial region 6 in $6L$ was longer in $2-6d$ than in $2-6c$, and region 7 in $6L$ was shorter by the same amount.

$2-6(6049) \times 2-6c$: Although the break points in chromosome 2 in $2-6(6049)$ were similar to those in $2-6b$, those in chromosome 6 were closer to the centromere than in either $2-6c$ or d . Thus, one of the 6^2 chromosomes in $2-6(6049) \times 2-6c$ was shorter than in the other crosses. Of 11 pachytene cells observed, 5 showed a homologously paired loop in the reversed "between breaks" segment in chromosome 2 (*e.g.*, Fig. 19), whereas in the other 6 cells this segment was non-homologously associated (*e.g.*, Fig. 20). Again this reverse pairing may be an effect of having one interchange segment that is very short. In the one cell with complete "pairing" and a cross configuration, there was extensive non-homologous association. In all the other cells, the distal region 1 in $2S$ did not pair but remained as a single thread. Thus, non-homologous association frequently occurred in the inverted segment when the extreme distal region of the same chromosome was unpaired, presumably due to an illegitimate progression of "zipper-like" pairing directed from region 8 in $6L$.

$2-6a \times 2-6c$: Unlike the previous type $1b$ combinations, this intercross

Fig. 22. $2-6c \times 2-6e$ (type $2a$): Top: diagram of normal chromosomes 2 and 6, arrows indicating the breakage positions for two interchanges $2-6c$ and $2-6e$; center: diagram of the four interchanged chromosomes in the F_1 intercross; and bottom: diagram of the pachytene configuration expected from synapsis of the interchanged chromosomes in the F_1 .

had the break points on the same arm in chromosome 2 and on opposite arms in chromosome 6. The expected pachytene configuration is similar to the diagram in Fig. 14, but with a smaller inversion loop formed by the "between breaks" segments. The inversion loop expected from homologous pairing was not observed but was replaced by non-homologous association (Fig. 21). In one cell an H-shaped configuration was observed. The test cross of an F_1 plant, $T2-6a Y PL/T2-6c y pl$, to a tester, $N y pl/N y pl$, gave 5.8% recombination between Y and PL , which are 31 units apart in the standard map of chromosome 6. This reduction in crossing over would not be surprising in view of the non-homologous association observed at pachytene.

Group 2 intercrosses

In group 2 intercrosses, breaks in the two interchanges are in the same arms of

both chromosomes. Although they are subdivided into types *2a*, *2b*, and *2c*, according to the relative break positions (Gopinath and Burnham 1956), the cytological configurations of the chromosomes at meiosis in F_1 plants should be essentially the same. As shown in Fig. 22 representing the constitution of the type *2a* intercross, $2-6c \times 2-6e$, each "pair" of chromosomes possesses a non-homologous intercalary part which corresponds to the "between breaks" segment. Therefore, two "pairs" with an intercalary loop are most likely expected at pachytene.

The present studies included two type *2a* combinations, $c \times d$, $c \times e$; two type *2b* combinations, $b \times 6052$, 6049×6052 ; and one *2c* combination, $b \times 6049$. Three of the five intercrosses, *i.e.*, $c \times d$, 6049×6052 , and $b \times 6049$ had only 10 "pairs" at diakinesis. At pachytene in $c \times d$, the "pairs" had no loops from the "between breaks" segments, and the members of each "pair" were associated throughout their lengths as if they were entirely homologous chromosomes. Similar configurations were observed in 6049×6052 but with an occasional small loop on the short arm of the chromosome 2 "pair".

In $2-6c \times 2-6e$ at diakinesis 77% of the cells had 10 pairs and 23% a ring of four plus 8 pairs. This result indicates a surprisingly frequent association of the four interchanged chromosomes at pachytene, which should have been the result of homologous pairing in the "between breaks" region 3 and/or 7. The length of region 3 was 19% of $2L$ and that of region 7 only 5% of $6L$. A cross-shaped configuration with a small loop at the junction of the "cross" at pachytene is illustrated in Fig. 23. The formation of "pairs" with intercalary loops is shown in Fig. 24. These loops were

Figs. 23-24. $2-6c \times 2-6e$ (type *2a*): 23, the pachytene configuration resulting from the synapsis of the four chromosomes. Note the small loop at the center of the "cross", which corresponds to the "between breaks" segment in chromosome 2. 24, two "pairs" of pachytene chromosomes $2^6c/2^6e$ and $6^2c/6^2e$. Note the fold in each "pair" produced on the longer member chromosome. The folded region failed to pair with the counterpart fold on the other "pair". $\times 1160$.

never found open but were closed by intimate non-homologous association.

Discussion

The cytological results obtained here point to the conclusion that there is a strong tendency for pairing to start at or near the ends of the chromosomes. That this tendency is not a phenomenon peculiar only to interchanged chromosomes is indicated by McClintock's studies (1933) of synaptic configurations of "B" type chromosomes, trivalents, and univalents, in which "ends of chromosomes tend to associate in advance of other parts of chromosomes, whether or not the ends are homologous". Rhoades (1952) also considered that the non-random association in his trisomic plants is accounted for if synapsis usually begins at the ends of the chromosomes. In the present study there were some intercrossovers in which the terminal regions of interchanged chromosomes often failed to pair. For example, an unequal "pair" was occasionally not attached at the distal ends. Also, synapsis of a terminal region in a complex of four chromosomes, for example in T2-6(6049) × T2-6c, appears to have been disturbed by synapsis in a neighboring region. Therefore, the general tendency for pairing to start at the ends may be upset by such factors as relative length and location of the region in relation to those of neighboring segments in chromosomes with structural rearrangements.

If the initial contact at the ends is an ordinary synaptic process in maize, what mechanism is responsible for this behavior? One of the possibilities is the operation of a long range specific attractive force which is stronger between the ends of chromosomes than other parts. The phenomenon of somatic pairing in *Drosophila* suggested to Hinton (1946) the need for the assumption of long range specific attractive forces as the underlying mechanism. Preferential contacts at the ends may occur when long segments of the chromosomes are differentiated into chromatic and achromatic zones that behave differently in pairing, as in the tomato (Brown 1949). In maize as well as in many other organisms, there is no cytologically observable special reason to assume the operation of a stronger attractive force between the ends.

A second possibility is an oriented or "bouquet" arrangement of chromosomes at the presynaptic stage. In most species of animals having a bouquet stage, synapsis usually starts at the polarized ends of the chromosomes. Oksala (1958) proposed the bouquet orientation of chromosomes in *Drosophila* in an attempt to unify the genetic data concerning the diverse interchromosomal effects. At zygotene in maize, the chromosomal threads form such a tight knot on the nucleolus that it has not been possible to determine the orientation of ends. McClintock (1933) suggested that as a result of their position in the previous anaphase "chromosomes with non-terminal fiber attachment regions are possibly in the shape of U's in many sporocytes at the time synapsis commences", since in univalents of mono-

somics, trisomics, and monoploids, the position at which most of the folding occurs is at or close to the spindle fiber attachment. Non-homologous associations might tend to commence not only at the ends but also between parts which are close together, *e.g.*, at the apex of the U. Thus, a concentration of foldback points at this positions would occur. The frequent occurrence of folding at or near the centromere was also noted in this study in the unequal "pairs" of interchanged chromosomes.

A simple mechanical explanation may serve the purpose as well if we assume that the chromosomes move about actively in the nucleus during early prophase. Then an end would have a mechanical advantage in pairing because it has more freedom of movement than the middle parts. In fact, the chromosomes of *Melanoplus* start to pair at their ends although in leptotene they are distributed throughout the nucleus without apparent polarization (Hearne and Huskins 1935).

The products of crossing over in non-homologously associated parts might result in a dicentric bridge and an acentric fragment in anaphase I, *e.g.* in the "pairs" in certain interchange crosses. The occurrence of crossing over in the folds might result in small ring-shaped chromosomes or a fragment. McClintock (1933) reported several instances in which modified chromosomes appeared in the progeny of aneuploid chromosomal types and suggested that the mechanism producing the changes may have been exchanges within paired non-homologous segments. No dicentric or other abnormal chromosomes expected from such exchanges were observed in the present study.

Summary

Cytological observations on intercrosses between stocks of maize interchanges involving the same chromosomes with different break points showed that at pachytene homologous terminal segments usually were paired whether the configurations were "pairs" or associations of four chromosomes. The intercalary segments showed extensive non-homologous association or asynapsis. In the crosses studied in which the break points were in opposite arms in both chromosomes, "pairs" in which the homologous intercalary segments including the centromeres were paired were never found. Hence, pairing usually began at the ends of the chromosomes, although it started, or occurred at the same time occasionally at other points along them. The intercalary segments were at a great disadvantage in pairing. The centromere played no apparent significant role in initiating pairing.

In certain intercrosses the frequent failure of pairing in the short terminal segment translocated to another chromosome was correlated with complete pairing in the adjacent region, indicating the importance of regions near but not at the end in controlling the pairing behavior.

Association initiated between two homologous regions continues to proceed along the chromosomes in a zipper-like manner, often bringing about

an association of non-homologous parts, until it is prevented by a counter association from the opposite direction.

The results of limited genetic linkage tests and spore quartet analyses of crossing-over frequencies showed that regions in which there was usually non-homologous association or asynapsis were characterized by reduced or no detectable crossing-over, whereas in a region that usually was paired, crossing over was essentially normal.

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