RELATION BETWEEN CHROMATID-TYPE AND CHROMOSOME-TYPE BREAKAGE-FUSION-BRIDGE CYCLES IN MAIZE ENDOSPERM

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BREAKAGE-FUSION-BRIDGE cycles have been rigorously proved to exist only in *Zea mays*, but there is every reason to believe that they occur widely. It is quite possible that they are universally produced by chromosomes broken in anaphase bridges. They may represent a major class of dominant lethals in genetic experiments and be responsible for the well-known observation that truly terminal deficiencies are not normally recovered in *Drosophila melanogaster*. A chromosome-type of breakage-fusion-bridge cycle has been described in the axolotl (DALTON and HALL 1950). In Agropyron, HAIR (1952) has described a chromosome-type breakage-fusion-bridge cycle in considerable detail. A similar chromosome-type breakage-fusion-bridge cycle has been found in Narcissus by DARLINGTON and WYLIE (1952). On other occasions, chromatin bridges persisting through several divisions have been plausibly attributed to breakage-fusion-bridge cycles of unidentified type. This is the case for the eggs of Habrobracon following irradiation of the sperm (WHITING 1945; ATWOOD, VON BORSTEL and WHITING 1956). KOLLER (1952) described a chemically induced tumor in the rat, which regularly had bridges, and ascribed by him to a chromosome-type breakage-fusion-bridge cycle. In the endosperm of Lilium BROCK (1954) has observed bridges almost certainly due to a breakage-fusion-bridge cycle. Finally, it should be noted that breakage-fusion-bridge cycles are probably an important mechanism in damage to growing tissues produced directly by radiation, as in the treatment of cancer.

Breakage-fusion-bridge cycles were first described by MCCLINTOCK (1938a). Chromatid bridges were generated at anaphase I of meiosis, from crossing over in an apocentric inversion, and the fate of the broken ends studied in gametophyte mitosis. In a series of papers by MCCLINTOCK since that date, many additional details were established; a brief general review, with diagrams of the two kinds of breakage-fusion-bridge cycle is given in MCCLINTOCK (1951). The first break initiating a breakage-fusion-bridge cycle can also be produced by a *Ds* element in the presence of *Ac*, or directly by radiation or some other mutagen. In the remainder of this paper, we shall simply use the word "cycle" as a convenient abbreviation for breakage-fusion-bridge cycle.

Two kinds of cycle are known, the chromatid type and the chromosome type respectively. The chromatid-type cycle results from a single break across one chromatid. This chromatid may consist of two strands which are broken at the

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same, or nearly the same level, the two free ends uniting. Alternatively, it might be considered that the chromatid is "single" at the time of breakage, but that when it doubles, the terminal element fails to duplicate, thus giving an equivalent sister union. The same result would be attained if the free ends are capable of rejoining immediately after duplication. Whatever its ultimate structure, the bridge that is produced at anaphase consists of one chromatid, which is either exactly or at least very nearly symmetrical about the preceding point of fusion.

The alternative chromosome-type cycle is initiated from a dicentric translocation. If the strands between centromeres are twisted through 180°, the anaphase figure will consist of two crossing chromatid bridges. With a 360° twist, or more half twists, interlocking chromatid loops result. These bridges break, and fusions occur between the ends of whole chromatids, thus re-establishing dicentric chromosomes in the two daughter nuclei.

It will be clear that each broken chromatid, in the chromosome-type cycle, could in principle undergo sister fusion, if its nature allows it to do so. If this were to happen, a chromosome-type cycle would be converted into two independent chromatid-type cycles. Conversely, two chromatid-type cycles might convert into a single chromosome-type cycle. The present paper is concerned with an experiment to test for the occurrence of this last event.

Information about cycles comes in part from direct cytological observations, in part from the phenotypes of the mosaics they yield. If the chromosome undergoing a cycle carries dominant markers, and the homologous normal chromosome carries the corresponding recessives, then a characteristic pattern is produced, as was first described by McCLINTOCK (1941b). While the geometry of the pattern varies widely, the *inclusion relation* of the loss areas, for a chromatid-type cycle, is a very definite one. It can be concisely stated in Set symbolism as: loss of distal marker $\supseteq$ loss of proximal marker (FABERGÉ 1956). This *inclusion relation* is simply a consequence of the breaking of a bridge which is symmetrical about its center with respect to the loci of the markers. Some infrequent accidents might upset this relation, such as breaking of a chromatid at several places, or perhaps the breaking of the sister strands at slightly different levels (McCLINTOCK 1945), but in practice such events are rare enough not to introduce any ambiguity. The inclusion relation does not necessarily hold for a chromosome-type cycle.

McCLINTOCK (1938a) showed that in the gametophyte, the chromatid-type cycle was the rule. In that paper, and in McCLINTOCK (1938b), it was shown that when two broken chromatids were introduced into the same nucleus, each of them continued, in the gametophyte, a separate chromatid-type cycle, and that fusions between broken chromatids to yield a chromosome-type cycle did not take place.

In contrast to the gametophyte, chromosome-type cycles were generated in the sporophyte when two broken ends were given to the zygote, one through the male, the other through the female gamete. This was first described by McCLINTOCK (1942), and later (McCLINTOCK 1943) an improved experimental arrangement yielded many more such unions. Earlier (McCLINTOCK 1938b) it had been shown

that the behavior of dicentric rings in the sporophyte required that the reunions of broken chromatids be of the chromosome, rather than of the chromatid or sister fusion type. This observation on ring chromosomes was later confirmed (McCLINTOCK 1941c).

If a single broken chromatid is introduced into the endosperm, it always undergoes a chromatid-type cycle. When introduced into a zygote, it will, ordinarily, stabilize; once stabilized, such a fresh chromosome end has the cytological properties of a natural chromosome end. However, this faculty of stabilizing a broken end may be under genotypic control, for in one experiment McCLINTOCK (1944a) observed among 188 cultures, four in which stabilization failed to occur, a chromatid-type cycle persisting throughout the development of the sporophyte. Chromosome-type cycles can also eventually stabilize in the late sporophyte development in maize (McCLINTOCK 1943). For this reason, it is to be expected that stable rod chromosomes should sometimes be recovered from ring chromosomes in maize, but so far this has not been observed (McCLINTOCK 1938b, 1941c).

The cytological possibilities of maize endosperm have intrinsic limitations, although bridges produced by cycles were demonstrated by CLARK and COPELAND (1940) and also by SCHWARTZ and MURRAY (in press). It is possible that bridges, particularly when short, tend to break early in anaphase and so escape detection.

McCLINTOCK (1941b) compared the endosperm mosaic patterns produced when one or when two chromosomes, each carrying the same dominant markers, have broken ends. Endosperm being triploid, such a comparison is conveniently made in a reciprocal cross, the broken chromosome being introduced either from the male or from the female parent. When two marked broken chromosomes were present, it appeared that the loss areas were larger than would be expected from a simple geometrical superposition of the patterns resulting from a single broken chromosome. Because of this apparent excess of loss area, McCLINTOCK suggested that the loss events in the case of two marked chromosomes might in fact not be independent. It was proposed that when two broken ends are introduced into the endosperm, they fuse and undergo a chromosome-type cycle, just as they had been proved to do in the zygote. Lack of independence in marker loss could then be brought about by a tendency for the chromatids of the double bridge to break at about the same level.

It has already been noted that the inclusion relation for marker losses does not necessarily apply to a chromosome-type cycle. The sister strand fusion of a chromatid-type cycle results in the bridge being symmetrical about its center with respect to the markers—with the possible rare exception of unequal breakage of the two strands. If a chromosome-type cycle is started by two broken chromosomes which are in every way identical, then the two bridges will also in the first instance be symmetrical, in the sense used above. The symmetry need not persist in later divisions, however, so that opportunities for departures from the inclusion relation will present themselves. McCLINTOCK's observation discussed in the preceding paragraph does not refer to such a departure, but only to a quantitative,

geometrical relationship. Looking for a departure from the inclusion relation, in the case of a chromosome cycle which was started as a symmetrical bridge would probably be very inefficient. A much more favorable situation would be created by a bridge that is asymmetrical from the outset.

In examining irradiated maize endosperm material, in which there were many mosaic kernels, it was noted that those attributable to cycles were, in the great majority of cases, of the regular types obeying the inclusion relation (FABERGÉ 1956). A plausible quantitiative consideration shows that most of them (about 89 percent) were probably taking place in the presence of other, unmarked broken chromosome arms. These would provide opportunities for fusions resulting in chromosome-type cycles that are from the beginning asymmetrical. While this radiation material provides no critical evidence, it suggests that chromosome-type cycles are not commonly formed in the endosperm. A preliminary description of the work presented here was given in FABERGÉ (1957).

MATERIALS AND METHODS

The aim of the experiment to be described here was to provide an opportunity for the formation of a chromosome-type cycle in the endosperm, in such a way that the event, if it occurred, could readily be recognized. The observations consisted in looking for a departure from the inclusion relation among marker losses in the mosaic. The positions of the breaks generated were such that any chromosome type cycle would from the beginning have bridges completely asymmetrical with respect to the markers. Such an experiment is easily made by means of MCCLINTOCK's (1949, 1951) displaced *Ds* stocks. Kernels of the constitution: *Ds C Sh Bz Wx/I Sh Bz Wx Ds/ I Sh Bz Wx Ds Ac/ac* were produced by making the cross: *I Sh Bz Wx Ds ac/ac* × *Ds C Sh Bz Wx/c sh bz wx Ac/ac*.

This experiment is similar in principle to the one described by MCCLINTOCK (1942, 1943) for the sporophyte, in that a broken chromosome is also introduced from the male and from the female gamete, and fusions between them looked for. An important difference is that in endosperm, because of the persistence of chromatid-type cycles, the opportunity for fusion is presented repeatedly at each cell division. In the sporophyte, on the other hand, this opportunity only occurs at zygote formation (or possibly in a few succeeding divisions). It will be noted that none of the crossover products can cause confusion. While there are four markers in the cross, in practice the relation between losses of *C* and losses of *Wx* is the critical one. Ideally, it would be possible to examine the same surface cells for both markers, but this is troublesome as the *C* anthocyanin pigment has to be bleached out before applying the iodine to detect *Wx*. It is more practical to make a very shallow cut, paring away the colored cells. This is legitimate, since the development of endosperm mosaics is chiefly radial, but the cut must be very shallow. To ensure the accurate superposition of the *C*-loss pattern with the *Wx*-loss pattern, holes about 0.08 mm in diameter were drilled in the vicinity of the areas being examined, and were filled with a fat soluble red pigment. These served as fiducial markers and can be seen on some of the illustrations. A vertical

illuminator was used for examining the kernels, and making Kodachrome records of typical cases. The illustrations (Figures 3–6) were made from the Kodachromes and are reproduced at a magnification of × 72.

RESULTS

About 1250 kernels of the critical constitution were obtained from a total of 8969 for the cross. Because their recognition depends on the presence of sufficiently large loss areas, the number is not exactly known. About 600 kernels had losses large enough to make detailed examination profitable and were actually used.

The two possible alternative kinds of chromosome behavior are illustrated in Figure 1. Starting with three homologous chromosomes broken at the *Ds* loci, the left side of the diagram shows each chromosome undergoing a separate independent chromatid-type cycle. The right side shows a paternal and a maternal chromosome fused to form a chromosome-type cycle; the remaining, third chromosome, is shown undergoing a chromatid-type cycle. It will be noted that at the stage when anaphase bridges are broken, the two sides of the diagram are identical, except that the broken chromosome ends may be nearer to each other in the case of the chromosome-type cycle. An opportunity for conversion of two chromatid-type cycles to a chromosome-type cycle is therefore presented at each cell division. For purposes of simplicity, the consequences of nondisjunction following bridge formation in endosperm (SCHWARTZ) will be disregarded at this stage and in the diagrams, but will be considered in the discussion.

Figure 2 shows one way in which a double bridge with asymmetrical strands in a chromosome-type cycle can break so as to give a loss of a proximal marker while preserving a distal one, or $L(C) \subseteq L(Wx)$ on the mosaic pattern. A chromatid-type cycle in the male parent chromosome can only result in $L(C) \supseteq L(Wx)$, with the exception of the possible rare events mentioned earlier. The relative lengths of the segments of the short arm of chromosome 9 are represented about in proportion to their pachytene length, but the long arm is purely diagrammatic.

A kernel of the constitution shown is initially colorless because of the presence of *I*, one dose of which is enough to inhibit color. Colored areas on the kernel show that both female parent chromosomes have lost *I*, through breakage of *Ds* in the standard position. It is therefore known that cells in colored areas each carry two broken ends in chromosome arms that no longer carry any markers. These colored areas, which in typical cases occupy between a quarter and a tenth of the entire kernel surface, themselves show pronounced mottling and twin spotting. This is typical of the marker *C* when involved in a cycle, since the intensity of anthocyanin color increases with the dosage of *C*. Thus, it is known that the male parent chromosome carrying the markers *C Sh Bz Wx* is undergoing a cycle initiated by the break at the distal *Ds* locus. This cycle is occurring in the same cells in which two unmarked broken chromosome arms are present, and which are themselves presumably undergoing cycles whose presence cannot be demonstrated phenotypically. If the broken end of the male parent *C*-chromosome should fuse with one of the unmarked ends, a chromosome-type cycle would be initiated, as illu-

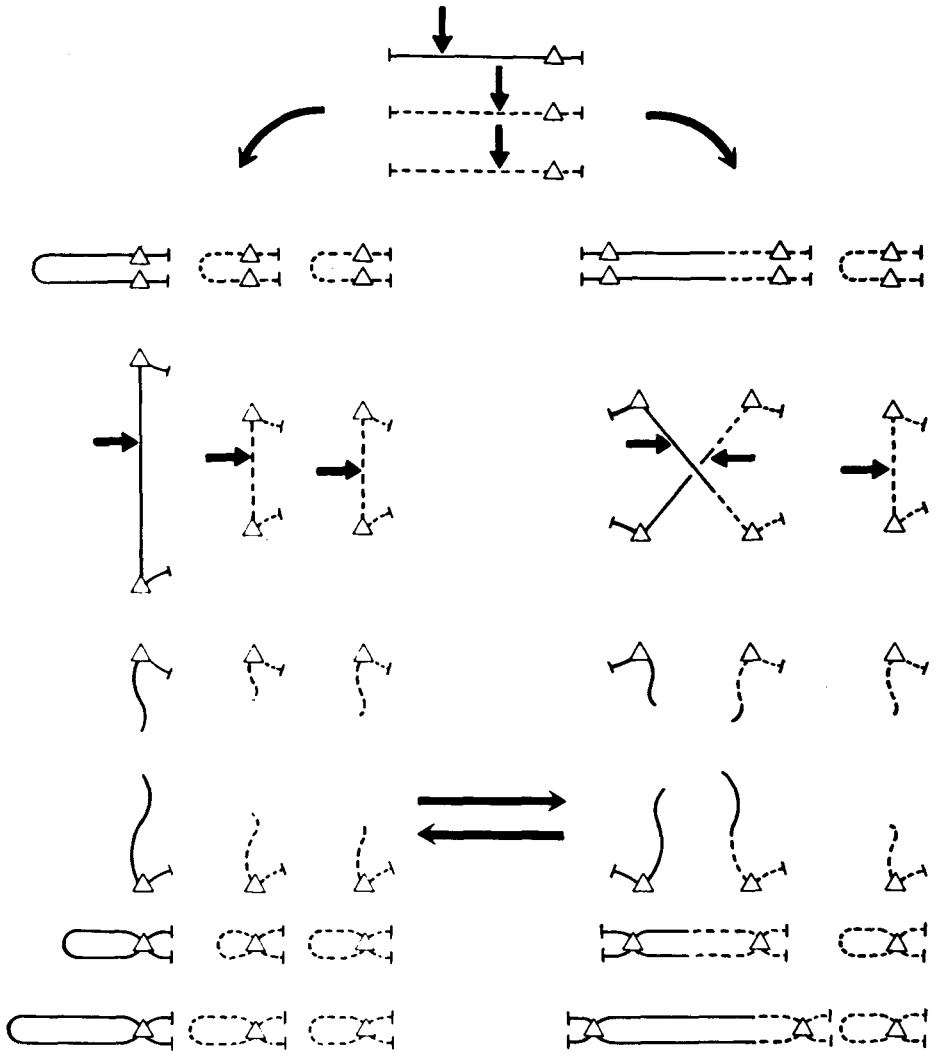


FIGURE 1.—Diagrammatic representation of the experiment. The male parent chromosome is shown in continuous line, the female parent chromosome in dotted line. On the left side, all three chromosomes are undergoing chromatid-type breakage-fusion-bridge cycles; on the right side, the paternal and a maternal chromosome have joined to form a chromosome-type breakage-fusion-bridge cycle. It will be noted that at the stage when bridges have broken, the two sides are structurally equivalent, so that a conversion as indicated by the large arrows is theoretically possible.

strated in the right side of Figure 1 and in Figure 2. Moreover, the opportunity for such a fusion is repeated at each cell division. In the case of a fusion occurring later, at some subsequent cell division, the relative lengths of some of the segments will differ from those shown in Figure 2, but the same principles will apply. Any bridge will be asymmetrical with respect to the markers.

The detectable phenotypic effect that may result from such a coalescence of

two chromatid-type cycles into a single chromosome-type cycle is the occurrence of a loss of *Wx* without previous loss of *C*. Many shallow cuts were made on colored areas and stained with iodine in the manner described, and no instances of such a loss of *Wx* underlying *C*-color were found. It is estimated that about 1000 cuts were made on approximately 600 kernels having sufficiently extensive colored areas. Since, at each cut, at least several hundred cells are examined, and losses of *Wx* as small as one cell are readily detectable, it can be estimated, as a rough order of magnitude, that if the event in question happens at all, it must be rarer than about one in 100,000 cell divisions. While this is a perfectly safe upper limit for the frequency, it seems impossible to make a closer estimate, because of the difficulty of assessing such subjective factors as the probability of not noticing a very small loss of *Wx* during the search. Moreover, this estimate of one in 100,000 cell divisions must certainly approach the frequency of various accidents in chromatid-type cycles, which were mentioned earlier, or the chance that a cut, while shallow, nevertheless went deep enough to uncover cells from a different cell lineage, or even mutation.

Associated with the colored regions in the kernels, were small colorless areas of obviously deficient cells. They were most often coupled with twin spotting, a darker colored area occurring by the side. The pattern of the cell outline shows that such areas were handicapped and grew more slowly than the surrounding tissue, as can be seen in Figures 3–6. These cells are homozygous deficient for all three ends of the short arm of the 9th chromosome, including the locus of *C*. Underlying such deficient, *colorless* areas, losses of *Wx* were often found. Several cases of this sort are illustrated in Figures 3–6. These small *Wx* losses were most often, of only three or four adjacent cells on the cross section, sometimes only one cell; a few as large as 10–12 cells were seen. They demonstrate that even quite small *Wx* losses in deficient tissue are readily detectable, and would undoubtedly have been seen under *C*-colored areas if they had occurred there. It would, more-

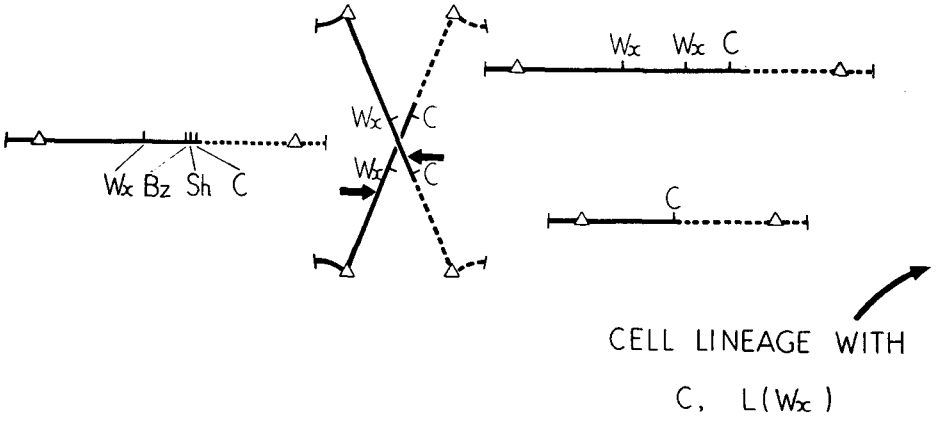
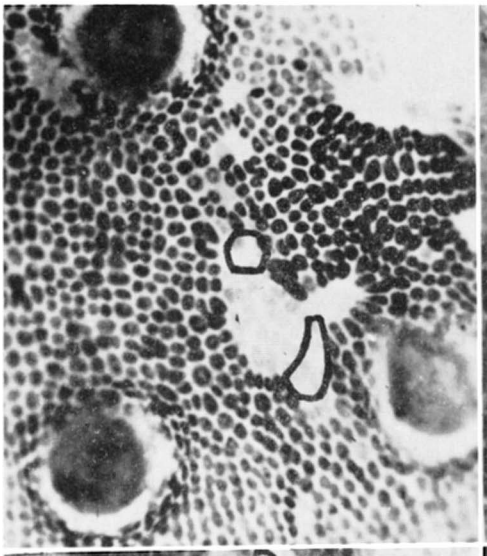
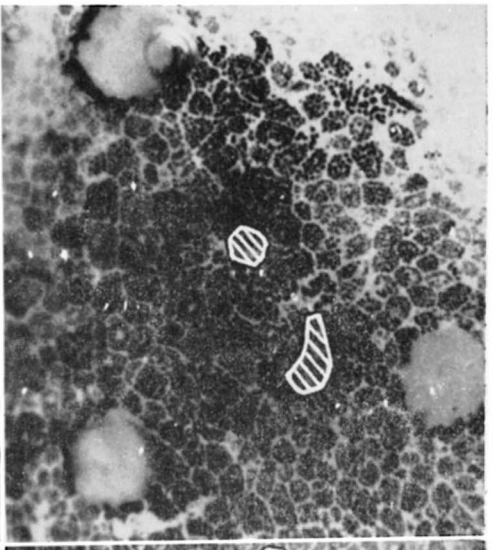


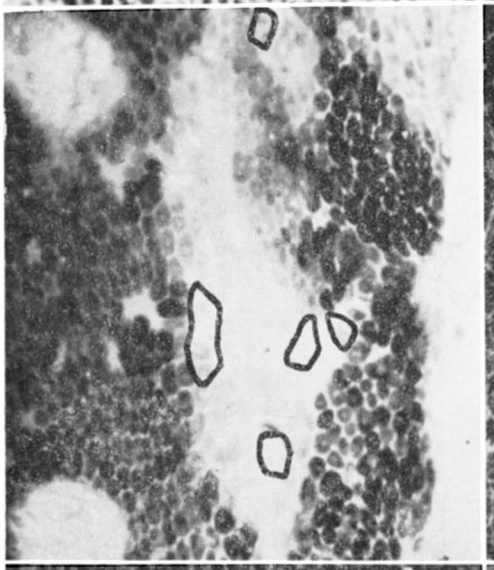
FIGURE 2.—Breakage of a double, chromosome-type bridge so as to yield the detectable event, loss of *Wx* without loss of *C*. The markers *C*, *Wx* are almost equidistant on the bridge.



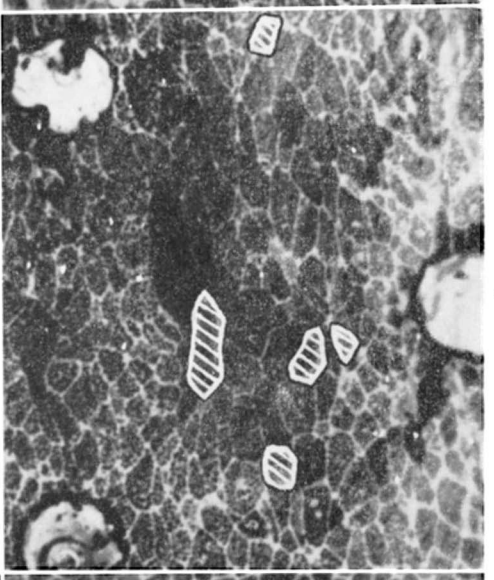
3A



3B



4A



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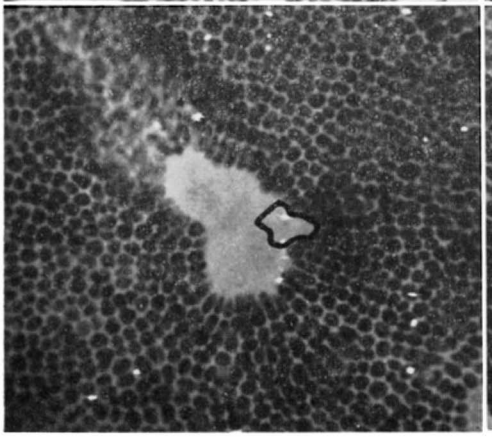

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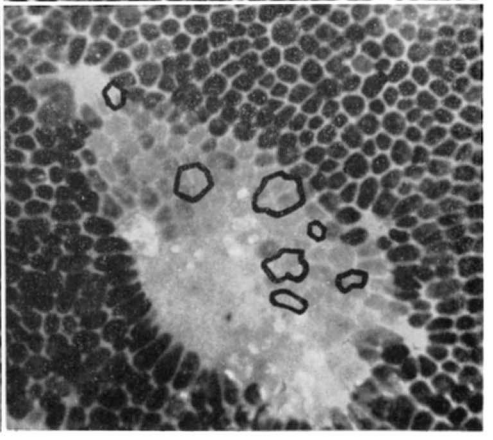

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over, have been expected that any such losses of *Wx* underlying *C* must be less handicapped on the whole, and therefore larger, since they would be homozygous deficient for a smaller part of the chromosome arm. This is an attempt to estimate the maximum frequency with which the phenotypic event might occur and still pass unrecognized. To pass from this to the actual frequency of formation of a chromosome-type cycle requires division by the probability that a double bridge breaks in such a manner as to produce the event $L(C) \subseteq L(Wx)$ on the mosaic. There is little sound basis for making such an estimate with any accuracy. If we assume that the probability of breakage is uniform throughout the entire length of each strand of the bridge, and consider the initial bridge, as illustrated in Figure 2, the probability of the critical event is 17.6 percent. This has to be multiplied by probability of a half-twist between the centromeres, though interlocking strands with an odd number of half-twists can also generate the critical event; in that last case the assumption of uniform distribution of breaks along the strand is perhaps rather less likely to hold. For bridges in later cell lineages, when the lengths of some of the segments would be different from those in the intial bridge, the probabilities will obviously be different. They may be greater or smaller. Mosaics clearly show that a bridge does not break in any regular position, but it does not follow that there is exactly uniform probability of breakage along the length. Departures from uniformity may again either increase or decrease the probability of occurrence of the critical event. The entire situation seems too complex to permit a realistic calculation on that basis.

There is, however, a much simpler and more satisfactory way of assessing the approximate probability of detection of a chromosome-type cycle in the experiment. It is based on the fact that the two markers *C* and *Wx* would lie nearly symmetrically in the initial dicentric bridge, and thus should be equally exposed to the probability of loss. It will be seen from Figure 2, that *C* and *Wx* are at about the same distance from the center of the bridge and from the centromeres. In later cell divisions this will change, but changes favoring loss of *C* will be equal to changes favoring loss of *Wx*. If the markers were exactly equidistant, then the probability of $L(C) \supseteq L(Wx)$ would equal $L(C) \subseteq L(Wx)$. Since $L(C) \supseteq L(Wx)$ is observable several times on each kernel, but the other type of event is not, it seems quite safe to conclude that $L(C) \subseteq L(Wx)$, if it ever occurs, must be rarer than one in several thousand.

It is concluded that when several broken chromosomes are present simultane-

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FIGURES 3–6.—Magnification ×72. 3A, 4A regions of aleurone surface with losses of *C*, underlying losses of *Wx* drawn in thick outline. 3B, 4B corresponding areas after paring off surface cells and staining with iodine; losses of *Wx* outlined. 5, 6 aleurone surface with losses of *C*, losses of *Wx* outlined. Large spots near margins are markers to ensure coincidence of photographs of surface with those of cut areas.

ously in maize endosperm tissue, each arm undergoes an independent chromatid-type cycle. A chromosome-type cycle is not formed between two such broken ends at a detectable frequency, in the way it is formed in the maize sporophyte.

DISCUSSION

It cannot be claimed that the behavior of broken chromosomes is fully understood even in maize. The general picture presented by a review of the literature is fairly complex and not entirely free of contradiction. It seems worth-while, nevertheless, to formulate some very tentative generalizations, in the hope that they may lead to further experiments.

An obvious question is why, under some conditions, chromatid-type cycles are formed, while under other conditions, a chromosome-type cycle is the rule. McCLINTOCK has touched on this question in several of the papers that have been quoted. A possible speculation is that this is related to effective singleness or effective doubleness of a chromatid. By *effective*, in this context, is to be understood *effective with respect to the possibility of sister strand fusion.* It does not necessarily mean that a chromatid, in some tissues, actually has only one strand while in others it has two or four. It might mean, for instance, that in one case the sister strands are prevented from fusing by a protective matrix, or by a special state of spiralization while in another case they are free to fuse.

It is clear that when a double, chromosome-type bridge has broken, the ends of sister strands are always much nearer each other than are the ends of whole chromosomes. Many different results in radiation work strongly indicate that initial separation of free ends is of critical importance in rejoining, and it may be remarked that in a crude kinetic model which considers free ends as independent particles, the time to contact will be some function of $(\text{distance})^{-3}$. While such models are unrealistic in disregarding steric considerations, they serve to demonstrate the great importance of initial separation. Thus, if sister fusion can occur at all easily, it ought to take precedence over chromosome fusion in cycles, and a chromosome cycle should convert to a chromatid cycle.

This may be the reason why a chromosome cycle is not formed in the gametophyte, a tissue in which McCLINTOCK (1938a) had reported suggestions of actual visible doubleness in chromatids. Such visible doubleness in anaphase chromatids has been seen in other materials by many workers, among whom might be mentioned NEBEL (1941) and MANTON (1945). It does not seem impossible that some of the double stranded bridges reported by SCHWARTZ and MURRAY (in press) are of the same nature. It is thus conceivable that the same considerations apply to early endosperm divisions as to the gametophyte. However, following nondisjunction, a single chromatid cycle can convert to a chromosome cycle in endosperm, at least in the later divisions, showing that a chromosome cycle can under these conditions compete against two chromatid cycles (SCHWARTZ and MURRAY in press). A chromosome-type cycle, even when initially symmetrical with respect to markers should, after some divisions, sometimes produce departures from the inclusion relation on the mosaic, since it seems unlikely that the two strands

of the bridge will always break at exactly the same level. Such departures being very rarely observable, it seems likely that most of the visible pattern is determined before nondisjunction occurs. This conclusion is reinforced by the consideration that nondisjunction would result in an area of loss of all markers at least equal to the area showing other losses, which is certainly not the case in the early, large scale, mosaic patterns. Many anaphases in endosperm show no visible bridges, but it is impossible to decide to what extent this may be due to failure of sister fusion or to early breaking of the bridge.

There are indirect indications from radiation data (FABERGÉ 1956) of a strong bias against interchromosomal exchanges in maize endosperm. This factor may be mainly responsible for the results presented here.

It would be out of place to discuss at length the relation of cycles to the behavior of radiation-induced chromosome breaks. As far as singleness or doubleness of strands is concerned, there is substantially nothing to add to MCCLINTOCK's (1938a) discussion. In the male gametophyte of maize, sister fusion always (or almost always) follows breakage at anaphase. In the corresponding stage of Tradescantia and some other plants, if breaks are induced at the "chromosome break" phase, that is, between meiotic telophase and about 30 hours preceding microspore metaphase, sister fusions are rare or absent. The chromosome behaves with respect to X-rays as though mainly single. Whether the rarity of sister fusions at this stage is due to a true stabilization of the breaks, or alternatively to sister fusion of *subchromatids* has never been established. If the last possibility is correct, bridges ought to appear in the pollen tube division following irradiation immediately after meiosis, but attempts to demonstrate them have failed because of technical difficulties (BISHOP 1950).

It is of course entirely possible that chromosome organization is different in maize and in the other plants mentioned. We would be reluctant to accept such a view without examining some other alternatives. In particular, it does not seem impossible to imagine a plausible model of chromatid structure which will be capable of passing from a double to a single phase. For instance, if a matrix is much less extensible than the strands embedded in it, these strands might be freed and approximated when the whole structure is stretched in a bridge, but effectively kept apart when not under tension.

A closely related question is that of the nature of true stabilization of free ends. It might be supposed that the necessary condition is simply a sufficiently long sojourn of a free end in the nucleus, in the unsaturated state. Because of the great difference in distance, it seems likely that sister fusion can follow breakage much more rapidly than does a chromatid reunion. It might thus be expected that in any cell division broken ends remain unsaturated much longer under a chromosome cycle regime than under a chromatid-type cycle regime. Thus, chromosome cycle conditions might be generally associated with the possibility of stabilization. The chromosome-type cycle of HAIR (1952) sometimes underwent stabilization in somatic tissues, just as in maize. It seems possible that the cycle in Narcissus (DARLINGTON and WYLIE 1952) also did so.

SUMMARY

An experiment is described whose purpose was to ascertain whether, in maize endosperm, separately broken chromosomes will fuse to generate a composite chromosome-type breakage-fusion-bridge cycle. Markers in the short arm of chromosome 9 were used, and breaks were induced by the *Ds-Ac* system. The markers and positions of breaks were such that if reunion between two broken chromosomes occurred, the event would be phenotypically recognizable on the endosperm mosaic. It was found that each broken chromosome end undergoes a breakage-fusion-bridge cycle (presumably initially of chromatid type) on its own and that fusion of different broken chromosome ends to give a composite chromosome-type breakage-fusion-bridge cycle does not occur in endosperm, at a detectable frequency. In this respect, endosperm differs from the sporophyte but is similar to the gametophyte.

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