THE MECHANISM OF MODULATOR TRANSPOSITION IN MAIZE[1]

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McCLINTOCK (1956) suggested that a transposable element in maize moves from the donor site to a different recipient site on the chromosome during the mitotic reduplication process. GREENBLATT and BRINK (1962, 1963) and GREENBLATT (1966) were able to offer experimental support for this idea, and further, developed a working hypothesis of a mechanism of the element's movement. Since the evidence collected by GREENBLATT and BRINK (1962, 1963) was based solely on their analysis of red-light variegated twin mutations occurring in medium variegated pericarp, it was not clear at that time whether the model accounted for the way in which all transpositions occur. In fact, it was believed that there might be two or more ways in which an element might transpose. It is the purpose of this report to present a new hypothesis of the mechanism of transposition and show that it is the only mechanism that explains all of the transposition data concerning the autonomous controlling element, Modulator, moving away from the *P* locus to other chromosomal sites.

Since Modulator *(Mp)* does not produce a direct effect on the maize phenotype, it has been studied by analyzing its interaction with the red pericarp allele on chromosome 1. The listing which follows serves to summarize the pertinent points that are known of this transposable element *(Mp)*—gene *(P)* interaction.

P^{rr}: This allele is of conventional chromosomal specificity on chromosome 1 conditioning a dominant red pigment in the pericarp, cob, and husk tissues (ANDERSON 1924).

Mp: Modulator is a transposable element which has no direct control of any recognizable plant phenotype, but is capable of moving autonomously from one chromosomal site to another during development of the plant.

$\overline{P^{rr}Mp}$: When *Mp* is located at the *P* locus the P^{rr} gene does not come to expression. However, in some cell lineages *Mp* leaves the *P* locus during the course of pericarp development, and in these pericarp cells where *Mp* is absent from P^{rr}, the chromosomal gene does come to expression and the red pigment develops. The resultant phenotype is known as medium variegated, and is characterized by a high frequency of red stripes on a colorless background (BRINK and NILAN 1952).

$\overline{P^{rr}Mp}$ + tr-Mp: When a transposed Modulator *(tr-Mp)* is included in a cell lineage which contains the $\overline{P^{rr}Mp}$ complex, the resultant pericarp phenotype ex-

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hibits red stripes, but with a markedly reduced frequency. This condition is known as light variegated and is believed to be due to the interaction of one Modulator with the other, causing a reduced frequency of transpositions (McCLINTOCK 1951; BRINK and NILAN 1952). The size of the red or light variegated sector in the pericarp indicates when the transposition of *Mp* away from *P* has taken place in the development of this tissue. That is, early developmental transpositions result in large somatic sectors while late transpositional events cause small sectors or stripes (ANDERSON and BRINK 1952). Red and light variegated sectors occur as twin sectors on medium variegated ears. The red sectors of these twin mutations may or may not carry a *tr-Mp* in their genome. The co-twin, light variegated, regularly carries a *tr-Mp* in addition to the $\overline{P^{rr}Mp}$ complex (GREENBLATT and BRINK 1962). The location in the genome of *tr-Mp* is most often within fifty recombination units of *P*. However, it is also found on chromosomes other than chromosome 1 in approximately 33 percent of the cases (VANSCHAIK and BRINK, 1959).

P^{wr}, P^{ww}: These are stable allelomorphs of P^{rr} conditioning colorless pericarp. In order to view the $\overline{P^{rr}Mp}$ complex alone in its transpositional behavior it is maintained as a heterozygote in a diploid nucleus with P^{wr} or P^{ww} (ANDERSON 1924).

Possible sequences of transposition: The major question concerning the mechanism of Modulator transposition is whether it moves only at a single specific time in mitosis or whether it can move at any or all stages of the mitotic cycle. Given the chromosome replication period as reference, is *Mp* transposed prior to, during, and/or after chromosome replication? There are four related periods during which *Mp* may transpose from the *P* locus, each of which leads to definable, potential consequences as to the pericarp phenotype (Figure 1). The hypothetical periods are: (1) Transposition from the *P* locus before any chromosome replication; (2) Transposition prior to *P* locus replication but after the receptor site has replicated (this requires the assumption that all sites within the chromosome complement do not replicate at exactly the same time); (3) Transposition after the $\overline{P^{rr}Mp}$ complex replicates but prior to the receptor site replication; (4) Transposition after all replication is complete but prior to cytokinesis.

In period (1) the only result in the final pericarp structure is a red sector which contains a transposed Modulator. The same final result in the pericarp is expected from period (2), with the modification that the red tissue of the sector would carry a *tr-Mp* in only half of its cells. Period (3) is expected to produce only red-light variegated twin mutations in the mature pericarp. Both the red sector and the light variegated sector of such twin spots are expected to always contain a *tr-Mp* element due to *tr-Mp* replicating a second time in conjunction with the receptor site (GREENBLATT and BRINK 1962). Period (4) has two different possible consequences in the final pericarp tissue. If *tr-Mp* migrates with the $\overline{P^{rr}Mp}$ complex to the same pole at anaphase, a potential twin spot with the red sector always totally void of *tr-Mp* is expected at the completion of the mitotic cycle. If, however, the single *tr-Mp* segregates with the P^{rr} chromatid, only an un-

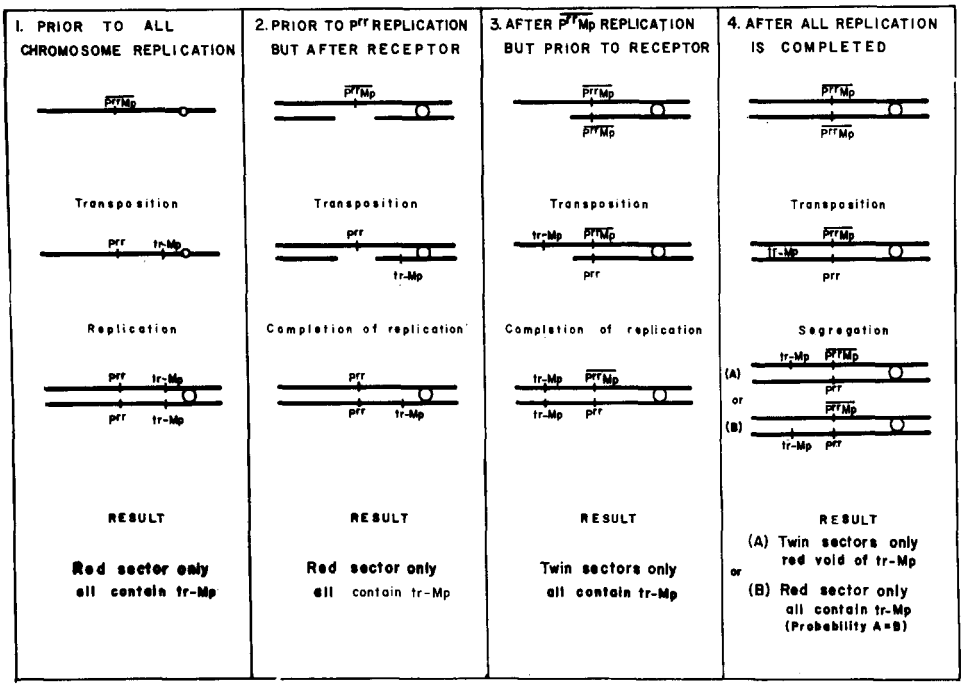

FIGURE 1.—Diagrammatic representation of all hypothetical sequences by which transposition of Modulator could occur during mitosis.

twinned red sector instead of a twin spot is expected in the pericarp. Of course, this sector will contain the *tr-Mp* element somewhere in its genome.

It should be noted that in all of the three ways in which untwinned red sectors in the pericarp could arise, they are always expected to carry *tr-Mp* somewhere in their genome.This contrasts with the postulated twinned red sectors which would be expected to contain a *tr-Mp* in the red co-twin less than 100 percent of the time. Direct measurement of the frequency of *tr-Mp* within twinned red sectors has shown them to be totally void of *tr-Mp* in approximately one third of the cases tested (GREENBLATT and BRINK 1962; present paper).

This difference in frequencies of *tr-Mp* constitutions between untwinned red sectors and twinned red sectors allows for a direct test of the occurrence of the genetic events responsible for untwinned red sectors if such events should occur. If selected untwinned red sectors in the pericarp are tested for their *tr-Mp* constitution (BARCLAY and BRINK 1954) only *tr-Mp* containing sectors should be found if any or all of the events outlined in Figure 1 occur.

In selecting such untwinned red sectors for analysis a problem arises because of the uncertain morphogenesis of the ear and the pericarp tissue. An untwinned red sector in the pericarp might come from a potential twin of which the light variegated co-twin in the three dimensional matrix of the ear is internal and not visible in the pericarp. By selecting morphologically untwinned red sectors for *tr-Mp* analysis, a concurrent and undesired selection is also made for red sectors

from twin mutations which have their light variegated co-twin "missing" (for a fuller discussion of this point see GREENBLATT and BRINK 1962). In spite of this drawback in testing for untwinned red sectors, a detectable difference between the two types of red sectors should still be measurable. Taking into account that: (a) untwinned red sectors resulting from potential transposition sequences 1, 2 and 4 (Figure 1) all carry a *tr-Mp* and (b) potential transposition sequences 3 and 4 (Figure 1) yield twin mutations expected to have approximately two thirds of their red co-twins carrying *tr-Mp*, the presumptive untwinned red class, even though diluted by the twinned red class, will be expected to contain more *tr-Mp* positive types than twinned red sectors alone. Thus, the expectation is to uncover a greater number of red sectors containing a *tr-Mp* when morphologically untwinned red sectors are selected than when visually identifiable red co-twins are selected.

RESULTS

Analysis of twinned and "untwinned" red sectors: To acquire large somatic red sectors for *tr-Mp* evaluation, a series of heterozygous medium variegated types were grown and pollinated by their respective inbreds carrying the P^{wr} or P^{ww} allele and known to be void of any Modulator element. The three inbred types involved were 4Co63, W9 and W23. Although the genetic background varied, the $\overline{P^{rr}Mp}$ complex came from a common source and was introduced to each of the inbred types by backcrossing.

Twinned red sectors had to meet two selection requirements; (1) that the twinned light variegated sector be present and contiguous, and (2) that the number of kernels in the sector be large in order to preclude any loss of *tr-Mp* by segregation to the nonfunctional meiotic products. "Untwinned red" sectors had also to meet two selection requirements; (1) that a light variegated sector of any detectable size be absent, and (2) that the positioning of the red sector in the pericarp did not preclude physical absence of a light variegated co-twin because of location at the tip or butt end of the ear. All of the kernels from the selected sectors were grown and the resultant plants tested for the presence of a Modulator element, anywhere in the genome, by the *Ds*-tester as outlined previously by GREENBLATT and BRINK (1962).

The results of these analyses are presented in Table 1. Part A pertains to three separate tests of twinned red sectors. On line 1 are listed 80 cases derived from inbreds 4Co63 and W9. These data were previously presented by GREENBLATT and BRINK (1962) and are republished here in order to compare with the W23 inbred type on lines 2 and 3. Of the total of 261 red twinned sectors tested for *tr-Mp*, 162 were found to contain the *tr-Mp* element while 99 were found to be totally void. The variation in *tr-Mp* containing red sector frequency is relatively small, showing a larger variation within an inbred type tested in two successive years than between different inbred types. The frequency of the *tr-Mp* containing class was found to be 62.1%, based on the total of 261 sectors tested.

In cases where the twinned red sector carries the *tr-Mp* element, the element

TABLE 1

Distribution of tr-Mp *among independent somatic red sectors occurring on medium variegated ears*

Stock	Total sectors	*tr-Mp* present		*tr-Mp* absent	
		Number	Percent	Number	Percent
Part A. Sectors are co-twins with light variegated					
4Co63, W9 (data of Greenblatt & Brink) 1962)	80	52	65.0	28	35.0
W23 (grown 1962)	110	65	59.1	45	40.9
W23 (grown 1963)	71	45	63.4	26	36.6
Total Pooled	261	162	62.1	99	37.9
Part B. Sectors are morphological non-twins					
W23 (Grown 1963)	94	58	61.7	36	38.3

is postulated to have left the *P* locus after the $\overline{P^{rr}Mp}$ complex replicated, and, furthermore, to have replicated at the receptor site a second time during a single cycle of reduplication. Proof of this sequence of events has already been given (GREENBLATT and BRINK 1962 and GREENBLATT 1966).

The results of testing 94 selected "untwinned" red sectors are given in Part B of Table 1. Strikingly, the percentage found to contain a *tr-Mp* is essentially the same as that found for the twinned sectors. This result is interpreted to mean that all those transpositional events which would lead to untwinned red sectors, all expected to contain a *tr-Mp* element, are not detectable even though selection was specifically made for them on a morphological basis. It would appear, therefore, that such types of transpositional events may not occur at all, for if they do the frequency of *tr-Mp* in the "untwinned" class would have been higher than that found for the twinned types. Indeed, one might ask if genetically untwinned red sectors occur?

Ratio of red:light variegated from heterozygous medium variegated: Another approach to the detection of presumptive red sectors which do not result from twin formation is to measure the frequency of red and light variegated types arising in the progeny of medium variegated parents. If all transpositions lead to potential twin mutations then the frequency of red : light variegated in an unselected progeny should be 1:1. If, in addition, transpositions occur which produce only red sectors then the frequency of the red class should exceed the light variegated class. These expectations would be true only if all potential types are recoverable in the progeny in unaltered frequency. As will be seen in the next section this is not the case.

Estimates of red:light variegated frequency have been published. Both BRAWN

(1956) and GREENBLATT (1966) have presented the relevant data from their work on variegated pericarp. Table 2 is a reprinting of these previous test data and they are here presented to show their significant points. Both BRAWN (1956) and GREENBLATT (1966) obtained red and light variegated progeny from identical matings, using the same genetic stock (medium variegated in W23 inbred background) mated to the pollen parent W23 P^{wr}/P^{wr}. The only differences in their procedures were the year in which the matings and progeny tests were made and the location. (BRAWN grew his material in Madison, Wisconsin, in 1955, while GREENBLATT grew his material in DeKalb County, Illinois, in 1962).

As seen in Table 2 both sets of data yield essentially the same results. The red class among the offspring in each sample is approximately 10% of the total; the light variegated class frequency is higher in BRAWN's data. These two sets of values are relatively close and are pooled in the lower section of the table. On the average, reds appear 10.22% of the time in the progeny while the light variegated class occurs only 7.41% of the time. This is a highly significant difference from equality. At first glance it appears that the two classes are not arising in equal frequency and that more reds are produced than light variegateds. The important question is whether or not this is true because of transpositional events or because of a modifying factor interceding between transposition (somatic mitosis of the parent generation) and the realization of the pericarp phenotype in the test progeny. Such a modifying influence would have to account for the total differ-

TABLE 2

Segregation of major colored pericarp phenotypes among the offspring arising from the mating W23 $\overline{\text{Prr}}\text{Mp}/\text{Pwr} \times \text{Pwr}/\text{Pwr}$

Pericarp phenotype*	Number of ears	Percent colored
	(Data of Brawn 1956)	
Medium variegated	3293	81.65
Red	411	10.19
Light and very light variegated	329	8.16
Total	4033	100.00
	(Data of Greenblatt 1966)	
Medium variegated	2301	83.43
Red	283	10.26
Light and very light variegated	174	6.31
Total	2758	100.00
	(Pooled from above)	
Medium variegated	5594	82.37
Red	694	10.22
Light and very light variegated	503	7.41
Total	6791	100.00

* The rare orange variegated type is omitted for purposes of clarity.

ence in measured frequency between the red class and the light variegated class. When only reds and light variegateds are considered, their pooled total is found to be 1197 individuals in these samples. The red class comprises 57.98% of these transpositional types while the light variegated class accounts for 42.02% of this grouping, so there is a calculated 15.96% difference between them. In other words, there are 15.96% fewer light variegated types than there are red types.

To explain this difference it is proposed that recombination between *tr-Mp* and the *P* locus in both the presumptive red types and the light variegated types occurs during meiosis of the parent generation. Recombination at this time reduces the realized number of light variegated types while not affecting the frequency of red types. This is to say, a $\overline{P^{rr}Mp}$ complex plus *tr-Mp* will yield a light variegated pericarp, but a $\overline{P^{rr}Mp}$ complex without a *tr-Mp* (expected to segregate with the homologous P^{wr} allele) will appear medium variegated and be classified along with the nontranspositional types. The red types are phenotypically identical in pericarp color with or without *tr-Mp*. Proof that such a recombinational loss can occur and that it is of sufficient magnitude to totally account for the difference between the red type and the light variegated type follows.

Recombination of tr-Mp *and the* P *locus:* Transposed Modulator and the *P* locus undergo recombination as evidenced by the presence of *tr-Mp* among P^{wr} progeny of a medium variegated parent (GREENBLATT 1966). To measure the frequency of this recombination a series of large red sectors was tested for the presence of *tr-Mp* in both the red and colorless (P^{wr}) plants which were grown from seeds taken from these somatic red sectors of medium variegated parents. The data resulting from employing a *Ds*-tester for *tr-Mp* detection are presented in Table 3. Part A of the table contains the results of testing two collections of independently occurring red sectors grown from the same inbred background, W23, in two successive years. These sectors were definite co-twins to light variegated sectors. Part B of the table contains the results of testing 55 independently occurring presumptive "untwinned" red sectors, also from the W23 background.

Comparison of the recombination frequency of *tr-Mp* and *P* in the two types of red sectors shows it to be the same. The differences found between the groups are no greater than the variability found within a group. Thus, by comparing the two types of red sectors, it is again seen that they can not be resolved as being different. Part C of Table 3 contains the pooled totals of parts A and B. Based on a total population of 2105 tested plants, the frequency of recombination between *P* and *tr-Mp* is estimated to be 17.1%. It should be noted that in both Parts A and B the number of red individuals totally void of a *tr-Mp* exceeds the number of colorless individuals containing the element. This excess is believed due to secondary transpositions which increase the dosage of Modulator in the red genome, and, as previously discussed by GREENBLATT and BRINK (1962), renders Modulator undetectable by the *Ds*-tester as used. It is convenient to view the red *tr-Mp* void class as a maximum estimate of recombination frequency while considering the colorless *tr-Mp* containing class as a minimum estimate.

TABLE 3

Number of plants carrying tr-Mp *among the segregants derived from independently occurring red sectors arising on medium variegated ears. Mating:* $P^{rr} +$ tr-Mp/$P^{wr} \times P^{wr}/P^{wr}$*

Part A. Sectors are co-twins with light variegated
Part B. Sectors are morphological non-twins
Part C. Pooled totals of Parts A and B

Stock	Total sectors (tr-Mp present)	Total Plants	Red pericarp		Colorless pericarp	
			Mp+	Mp−	Mp+	Mp−
Part A						
Inbred W23	..	...	287	175	143	271
grown 1962	65	876	(32.8)**	(20.0)	(16.3)	(30.9)
Inbred W23	..	...	164	127	77	198
grown 1963	45	566	(29.0)	(22.4)	(13.6)	(35.0)
Part B						
Inbred W23	..	...	225	108	89	241
grown 1963	58	663	(33.9)	(16.3)	(13.4)	(36.4)
Part C						
Total	..	...	676	410	309	710
pooled	168	2105	(32.1)	(19.5)	(14.7)	(33.7)

* Each of the resultant progeny were in turn pollinated with a *Ds* tester.
** Number within parenthesis is percentage of total of number directly above.

The measured recombination value of *P* and *tr-Mp* derived from these red sectors serves to estimate the loss of *tr-Mp* from the genome of presumptive light variegated types. GREENBLATT and BRINK (1962, 1963) have already shown, with linkage analysis of *tr-Mp* from red and light variegated co-twin sectors, that the locations of *tr-Mp* are the same in both types. Thus, a random sample of *tr-Mp* sites provided by the red sector analysis, serves to estimate the recombination behavior of *tr-Mp* in a random sample of light variegated types. Therefore, the total deficit of the light variegated class from the progeny of heterozygous medium variegated individuals is totally accounted for by this recombinational loss.

At the time transpositions occur potential light variegated pericarp cells are formed in equal frequency with potential red pericarp cells. This is to say that all transpositions produce *only* twin mutation types and the possible transpositional events which have untwinned red sectors as a consequence *do not* occur.

Twin mutations do not always result in twin sectors; untwinned sectors are found on medium variegated ears. In order for visible red-light variegated twin spots to appear, both original primordia must come to lie side by side in the pericarp.

The mechanism of transposition: The restriction that all transpositions produce only potential twins serves to eliminate three of the four hypothetical ways in which *Mp* can transpose. In Figure 1 it can be seen that alternatives 1, 2 and 4 produce potential untwinned red sectors which do not occur. Only the third

possibility remains. However, this possibility must be modified to account for those twin mutations which do not carry a *tr-Mp* element in the red co-twin. With two restrictions, (1) only twins are possible, and (2) some red co-twin sectors may be void of *tr-Mp*, a completely definable sequence of events involved in the transposition is made possible. An outline of these events follows:

1. Modulator must only transpose after the $\overline{P^{rr}Mp}$ complex is replicated. If *Mp* transposed prior to $\overline{P^{rr}Mp}$ replication only untwinned red sectors would result. 2. The time at which the $\overline{P^{rr}Mp}$ complex replicates is the same time at which the entire chromosome complement is reduplicating. Some chromosomal sites, however, have not as yet reduplicated. 3. Only the newly formed copy of *Mp* transposes. The *Mp* conjoined with the parent chromatid does not move. If it did, untwinned red sectors would result. 4. The new *Mp* copy can only move to a site on the parent chromatid (its own parent chromatid or a nonhomologous one). Again, if it moved to a new strand only red sectors would occur. 5. At the receptor site *tr-Mp* may serve as a template and replicate again when the receptor site replicates or, it may not replicate a second time during a single mitosis.

The expected frequency of *tr-Mp* not replicating a second time is 37.9% of the time (Table 1). In such cases, when the receptor site is on chromosome 1, *tr-Mp* is on the old strand and mitotically passes to the daughter cell along with the original $\overline{P^{rr}Mp}$ complex (potential light variegated). The other daughter cell receives only an *Mp* void chromatid with a P^{rr} gene (a potential co-twinned red). If, however, *Mp* transposes to a site on a nonhomologous chromosome (33% of the cases as measured by VANSCHAIK and BRINK 1959) by random segregation, it would be included in the daughter cell with a $\overline{P^{rr}Mp}$ complex 50% of the time and the other half of the time with a P^{rr} allele. This is the only way in which an untwinned red sector containing a *tr-Mp* can be anticipated to form. The expected frequency is .379 (when *tr-Mp* does not replicate a second time) times .33 (when the receptor site is on a nonhomologous chromosome) times .50 (random mitotic segregation of chromosome 1 chromatids with nonhomologous chromatids) which equals .0625 or 6.25% of the time. Thus, at least 93.75% of the time, transpositions result genetically in potential twin mutations.

DISCUSSION

The major difficulty in analyzing transpositional events during the mitotic cell divisions which build the pericarp tissue (and the sex cell lineages) is that the results of these events can not be recovered until the tissue is fully formed and mature. Compounding this difficulty is the fact that many of the phenotypic consequences of transposition can not be interpreted with respect to the presence or absence of a Modulator element in the genome of the resultant pericarp but must await a progeny test by means of the *Ds*-tester. Thus, superimposed on the transpositional sequences are factors of morphogenesis, meiotic recombination, and secondary transpositions.

In spite of these difficulties it appears that it can be documented that all trans-

positions result in potential twin sector formation. As presented in Table 1, the selection for the presence of apparent untwinned red sectors, based on their expected Modulator composition, proved to be without success. In addition, the data in Table 3 show that the recombination frequency of *tr-Mp* with *P* fully accounts for the difference from equality when the frequency of red:light variegated types is directly measured.

Large morphologically twinned red-light variegated sectors are obvious when they occur in the pericarp of the ear but are not so obvious when their size is reduced. However, morphologically late occurring (small) twin spots can be found. They appear, on the surface of the pericarp, as colorless tissue adjacent to red stripes less than one kernel in size. Such twinned stripes are found bordering pericarp tissue still exhibiting the high frequency of later transpositions (numerous thin red stripes) characteristic of a single Modulator element leaving the *P* locus.

The postulated model of transposition requires that the newly duplicated copy of Modulator on the then forming daughter chromatid transposes, and that the original $\overline{P^{rr}Mp}$ complex remains intact. Otherwise untwinned red sectors would be produced. While this sequence accounts for the absence of untwinned red sectors it also provides an insight into why the element can move from place to place on the chromosome while, for the most part, leaving the linear continuity of the chromosome intact. It is possible that the linear tie-up of the newly formed daughter chromatid is not yet complete at the time *Mp* transposes, and that after it leaves the donating site the coupling of the new chromatid copy comes to completion. If Modulator is pictured as being within the linear continuity of the chromatid thread, as lambda prophage is believed to be in *E. coli* (CAMPBELL 1964), then a problem arises as to how the transposing element attaches to the parental chromatid at the receptor site. It seems easier to picture the *Mp* element as synapsed with the main axis of the chromatid rather than coupled within it. What holds the element to the chromatid and what holds the multifibrils of a chromosome together remains unknown.

It is known that the frequency of *Mp* transposition from the *P* locus can drop to zero in certain cell lineages. Such cases yield a colorless (no stripes) phenotype in the pericarp and are known as "mutant white." BRINK (1958) has demonstrated that this does occur, but its frequency, judging from the frequency of mutant white progeny of a heterozygous medium variegated parent, is very low when compared to the red class frequency. It might well be that just such a stable conjoined relationship of the element with the chromosome represents a modification of the synapsed condition to a stage where the element is inserted directly into the chromosome.

Most transpositions have no phenotypic effect detectable at the *P* locus, so that when the independently occurring red types are compared with each other they are phenotypically the same. Rarely, an atypical red type is found (i.e. a dilute red color instead of the intense dark red found in the same inbred background).

This lack of frequent modification of the chromosome by the transposition of the *Mp* element supports a synaptic model of the conjoining.

As has already been noted, two classes of twin mutations occur: those whose red sector contains a *tr-Mp* element and those whose red sector is totally void of a *tr-Mp* element. The data presented in Table 1 show that they do not occur in equal frequency but that some 62% contain the *tr-Mp* element somewhere in the genome. The proposed model of transposition does not directly account for this frequency but does suggest a possible explanation which is based on the extent of replication of the receptor site.

Since only twin mutations occur at the time of transposition, the Modulator element must be received by the old strand and not the strand undergoing synthesis. It is at the receptor site that Modulator may or may not undergo a second replication. If it does replicate a second time a *tr-Mp* element is included with the new strand and the resultant potential red sector will contain a *tr-Mp* element. The problem, therefore, involves those conditions which govern this second replication. A plausible explanation is that though potential receptor sites have not as yet replicated (i.e. a fully formed new copy of the site is not available), these sites are not all in exactly the same stage of replication. If enough time and substrate are available the newly arrived *tr-Mp* functions as a template and the new copy is included in the new strand. If it is too late to function as a template but early enough to conjoin at the receptor site, then the new strand is void of *tr-Mp*. If this is the case, then the relative extent of replication of the receptor site should be referable to the *P* locus since it has already replicated. Some preliminary data (GREENBLATT 1963, and unpublished) indicate that the receptor sites at which replication does not occur a second time are predominantly very close to the *P* locus. Those receptor sites at which a second replication does occur, while in some cases equally close to *P*, are in the main, more loosely linked with *P*. This then suggests that those sites near *P*, at the time of its replication, are closer to completing replication than more distant sites and while serving as receptor locations do not allow the second replication. The total observed frequency of 62% second replications would then be definable in terms of proximity to the *P* locus (only because this is where *Mp* starts from—any site in the genome presumably will serve in the same manner if *Mp* is initially conjoined there). However, proximity difference also involves probability of sites functioning as receptors. The further a site is from *P* the lower the probability it will function as a receptor (VAN SCHAIK and BRINK 1959; GREENBLATT and BRINK 1962).

Whether the sequence of events postulated for Modulator transpositions can also account for the transposition of other, different, transposable elements (*Spm*, MCCLINTOCK 1956; *Dt*, RHOADES 1941; *En*, PETERSON 1961) has not been directly tested, but there is no reason to presume that it does not. MCCLINTOCK (1956) working with the nonautonomous type element, *Ds*, known to transpose only when Activator (Modulator and Activator appear to be the same element studied at different chromosomal sites, BARCLAY and BRINK 1954) is present, concluded that upon transposition of *Ds*, the *Ds* element that was inserted into the

new location came from only one of the two sister chromatids. Insertion of the *Ds* at the receptor location was accompanied by its removal from the previous location. It seems reasonable, therefore, to suppose that this model of the mechanism of Modulator movement is applicable to all transposable elements, of both the autonomous and nonautonomous types, which can change position without change in the specificity of the element or the chromosome. In the case of Modullator at the *P* locus the vast majority of cases are simple transpositions without change in the specificity of the element or the chromosome.

SUMMARY

Red and light variegated pericarp phenotypes occur as the most frequent mutants (10.2% and 7.4% respectively) among the backcross progeny of medium variegated pericarp maize. Both mutant types also frequently occur as morphological twin spots in pericarp tissue. The genetic basis of these mutant types is now recognized as the result of transposition of the Modulator element away from the *P* locus to some other chromosomal site elsewhere in the genome. Transposition occurs during mitosis. As the result of transposition potential red and light variegated cell lineages can only be produced in equal frequency. Recombination of the transposed Modulator and the *P* locus during meiosis results in fewer light variegated types than red types among the offspring. These findings suggest that: (1) Transposition occurs only when the chromosome and its conjoined *Mp* is replicating; (2) Only the new copy of *Mp* transposes; (3) The receptor site of *tr-Mp* must not as yet have replicated at the time of transposition; (4) *Tr-Mp* may replicate a second time along with the receptor site (62% of the cases).

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