TRANSPPOSITIONS OF MODULATOR, A COMPONENT OF THE VARIEGATED PERICARP ALLELE IN MAIZE¹

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GENES, in the classical sense of the term, have fixed chromosome positions that can be determined by linkage tests with other genes. These units change position in relation to the genes on either side only as a result of chromosomal rearrangements. McCLINTOCK (1951) discovered genetic elements in maize that do not regularly occupy the same position in the genome but are capable of undergoing transposition from one locus to another by some mechanism other than ordinary chromosomal rearrangement. Modulator (*Mp*) an element associated with variegated pericarp and cob in maize (*P^{vv}* in EMERSON'S terminology, 1917) is such a transposable unit. *Mp* is similar in action to, or identical with, a factor which McCLINTOCK termed Activator (*Ac*).

Modulator was interpreted by BRINK and NILAN (1952) as a factor which, when present at the *P* locus in conjunction with the *P^{rr}* gene (self-red pericarp, red cob) suppresses pigmentation. *P^{vv}*, therefore, may be equated to $\overline{P^{rr}Mp}$. Removal of *Mp* from the $\overline{P^{rr}Mp}$ complex results in full color expression of *P^{rr}*. The ear phenotype termed medium variegated, which comprises numerous red stripes of various sizes on a colorless background, was considered to be the result of sporadic losses of *Mp* from the *P* locus in somatic tissue in plants heterozygous for variegated and a colorless pericarp allele. Progeny tests show that another, less conspicuous but about equally frequent, mutation called light variegated accompanies the mutations to self-color. Light variegated pericarp plants were found to differ from medium variegateds in possessing an additional Modulator (transposed Modulator = *tr-Mp*) at some position in the genome other than the *P* locus. This genotype may be designated, therefore, as $\overline{P^{rr}Mp}/P^{vv} + tr-Mp/-$. Evidence from twinned red and light variegated sectors on medium variegated ears, and from other sources, points to the conclusion that the second Modulator (*tr-Mp*) present in light variegated arises by transposition of *Mp* to one or another site when variegated mutates to self-red at the *P* locus. Transposed Modulator reduces the frequency of *Mp* losses from the *P* locus in $\overline{P^{rr}Mp}$ plants about 60 percent (BRINK 1954), thus resulting in the light variegated phenotype.

The present study deals with the distribution of the sites to which Modulator is transposed when the element is removed from the *P* locus in the mutation of

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$\overline{P^{rr}Mp}$ to P^{rr} . The criterion used to identify plants carrying $tr-Mp$ was the capacity of this element to change the variegated phenotype from medium to light.

MATERIALS AND METHODS

The variegated pericarp allele used was derived originally from a single plant heterozygous for colorless pericarp and cob. It was introduced into a few locally adapted inbred dent strains, at least three backcrosses to the respective recurrent parent lines having been made before the present tests were begun.

A series of independently occurring mutations from medium to light variegated were assembled in these inbred strains by propagating sublines from (1) single light variegated ears in otherwise medium variegated families (2) light variegated sectors on medium variegated ears (3) light variegated sectors that were twinned with self-red mutations, and (4) single-kernel light variegated mutants on medium variegated ears. Each of the light variegated mutants thus isolated (heterozygous for the variegated pericarp allele and hemizygous for transposed Modulator) was mated at once with a colorless pericarp inbred strain. Progenies were then grown out, and the open-pollinated ears were harvested and classified for pericarp color. This direct testing procedure reduced to a minimum the opportunity for secondary transpositions of $tr-Mp$ to occur; and the uniformity of genetic background, incident to the use of inbred parental lines, facilitated identification in the testcross families of the two main classes of offspring, light and medium variegated plants.

As noted earlier, plants heterozygous for colorless pericarp and the variegated allele are medium variegated, whereas addition to this genotype of transposed Modulator in single dose changes the phenotype to light variegated. If $tr-Mp$ is located at a position not linked with P , then by random assortment of $tr-Mp$ and P half the variegated plants resulting from testcrossing such light variegated heterozygotes will be light and half will be medium. If $tr-Mp$ is linked with P , then more than half the variegated segregates will be light, the higher the percentage of individuals in this class, the closer the linkage indicated.

Preliminary to the above mentioned study a series of light variegated mutants, that had appeared in our cultures earlier and had been propagated through two or more additional generations, were crossed with stocks carrying reciprocal translocations marking most of the 20 chromosome arms. These matings were made with a view to determining the distribution of transposed Modulators, wherever the latter were situated in the genome. Two facts soon came to light that led to a change in this rather unwieldy experimental plan. It was found that, after propagation of a given light variegated mutant through a generation or so, position in the genome of transposed Mp often varied from one subline to another, presumably as the result of secondary transpositions. Furthermore, in a rather high proportion of the independently occurring mutants it was observed that $tr-Mp$ was present on chromosome 1, linked with P . Attention was then redirected to newly arisen mutations of medium to light variegated and to the determination

among these mutations of the relation of *tr-Mp* to the *P* locus only, as outlined earlier in this section of the report.

*Validation of the method used for estimating linkage of transposed
Modulator with the P locus*

The method employed in estimating the amount of recombination between transposed Modulator and the *P* locus in the present investigation was applicable to the variegated pericarp segregates only, following testcrosses with colorless pericarp of light variegated plants heterozygous for colorless pericarp and hemizygous for transposed Modulator. The light variegated phenotype ($\overline{P^{rr}Mp}/P^{ww} + tr-Mp/-$) served as the criterion for the presence of transposed Modulator in contrast to medium variegated ($\overline{P^{rr}Mp}/P^{ww}$) in which *Mp* is present in the genome as a component of the variegated allele only. Very light variegated plants (occurring as mutants with an over-all frequency of roughly three percent of all colored segregates) were included in the light variegated class on the grounds that they usually arise from the latter genotype and differ only in possessing an additional *Mp* element (BRINK 1954). Mutations of variegated to self-red pericarp, which occur with a similar low frequency, were not scorable for the presence or absence of *tr-Mp* by the method in question, and so were omitted from the computations. This procedure, it will be noted, leaves out of consideration all the colorless pericarp individuals, comprising one half the testcross populations. The question may properly be asked whether a valid estimate of the amount of recombination between *tr-Mp* and the *P* locus can be obtained from the variegated segregates only.

Conceivably, linkage between *tr-Mp* and the variegated pericarp allele, is spurious in part as a result of the two *Mp* units present in the nuclei of light variegated plants tending to pass to the same pole at the heterotypic division in meiosis regardless of the location of *tr-Mp* in the genome. That such preferential assortment does not occur was demonstrated by the following experiment.

Testcross families representing 23 independently occurring mutations from medium to light variegated were reared under conditions in which the colorless pericarp individuals, as well as the variegateds, could be scored for presence and absence of *tr-Mp*. If the two *Mp* units involved do not assort preferentially then estimates of the distribution of *tr-Mp* within the respective colored and colorless classes should correspond to each other.

The 23 light variegated mutants, heterozygous for colorless pericarp, and hemizygous for transposed Modulator ($\overline{P^{rr}Mp}/P^{ww} + tr-Mp/-$) were mated with a colorless pericarp (P^{ww}) inbred strain not carrying *Mp*. These stocks were homozygous for colorless aleurone (*cc*). The testcross offspring were reared in an isolation plot and, following detasseling, were pollinated by a strain carrying Dissociation (*Ds*) at the standard position on chromosome 9 (McCLINTOCK 1953) and also the dominant aleurone color factor, *C*, in a distal location on the same chromosome arm. The detasseled plants were scored at maturity both for pericarp color and the presence or absence of *C* to *c* mottling in the aleurone. The

C to *c* mottling occurs as the result of losses to the *C Ds/c ds/c ds* aleurone nuclei of the chromosome fragment bearing the dominant *C* marker, by virtue of breakage at the *Ds* locus, thus giving rise to lineages of colorless cells. Such breakage takes place only when both *Mp* and *Ds* are present in the nucleus. Thus the *C* to *c* mottling provides a specific test for occurrence of *Mp* (presumably at any locus) in the genotype. The question at issue is the extent to which the distribution of *tr-Mp* in the colorless pericarp class of segregates, as thus determined, corresponds with the proportion of light and medium variegateds among the colored offspring.

The relevant data are summarized in Table 1. Inspection of the numerical results shows that (1) the amount of recombination indicated by both criteria varies widely from family to family in this group and (2) estimates of this value based upon the proportion of colorless offspring with and without *tr-Mp* correspond reasonably well in each case to that which would have been obtained had the numbers of light and medium variegated segregates alone been recorded. The regular correspondence between the distribution of *tr-Mp* between the colored and colorless pericarp classes within families shows that any tendency for the two *Mp* units present in the light variegated genotype to assort together in meiosis can be no more than a minor factor conditioning the proportion of medium and light variegated segregates if, indeed, it is operative at all.

RESULTS

Preliminary tests for distribution of tr-Mp throughout the genome

The 350 testcross families scored for light and medium variegated and for one or another of a series of reciprocal translocations marking most of the 20 chromosome arms showed that *tr-Mp* can be found in a variety of positions in the genome both linked and nonlinked to the *P* locus. It was apparent from these data also that, in terms of total length of the chromosome complement, *tr-Mp* was linked with *P* on chromosome 1 in a disproportionately large number of cases. Linkage was definitely established in two cases to reciprocal translocations not involving chromosome 1. In one of these cases *tr-Mp* showed about 34 percent recombination with T5-9a, and in the other about 30 percent recombination was found with T4-5b. Data from another group of families showing linkage between *P*, *tr-Mp*, and one or another reciprocal translocation involving chromosome 1 suggested that *tr-Mp* was located on the respective complementary chromosome involved in the exchange. The translocations giving such evidence were T1-3a, T1-4b, T1-2d, and T1-5b. Thus evidence was obtained that *tr-Mp* can occupy positions on chromosomes 2, 3, 4, 5, and 9, as well as various positions on chromosome 1.

Tests of newly arisen mutations to light variegated

The results of testing for recombination between *P* and *tr-Mp* of new mutations to light variegated are summarized in Table 2. The groups of mutations originally

TABLE 1

Distribution of transposed Modulator among colorless pericarp offspring in relation to proportion of light and medium variegated segregates following testcrosses with colorless of light variegated plants heterozygous for colorless and hemizygous for tr-Mp

Family	Number of plants					
	Colored pericarp			Colorless pericarp		
	Light var.	Medium var.	Percent medium	present	<i>tr-Mp</i> absent	Percent present
73- 1	27	29	51.8	28	40	41.2
73- 2	31	30	49.2	27	31	46.6
73- 3	54	44	44.9	36	62	36.7
73- 4	32	7	17.9	7	26	21.2
73- 5	17	20	54.1	20	13	60.6
73- 6	72	4	5.3	3	64	4.5
73- 7	39	12	23.5	13	35	27.1
73- 8	38	2	5.0	0	34	0
73- 9	48	36	42.9	38	49	43.7
73-10	28	19	40.4	19	32	46.3
73-11	54	0	0	1	51	1.9
73-12	54	0	0	5	62	7.2
73-13	91	1	1.1	3	92	3.2
73-14	24	1	4.0	3	15	16.7
73-15	13	23	63.9	11	17	39.3
73-16	25	19	43.2	20	21	48.8
73-17	17	19	52.8	28	22	56.0
73-18	28	29	50.9	22	29	43.1
73-19	46	10	17.9	13	45	22.4
73-20	21	12	36.4	21	22	48.8
73-21	36	39	52.0	29	38	43.3
73-22	58	3	4.9	4	46	8.0
73-23	44	2	4.3	3	60	4.8

detected as twinned with a red pericarp sector, single kernels, or entire light variegated ears appeared not to show different recombination values, and so are considered together. Of the 87 families tested, each representing an independent mutation to light variegated, 56 showed linkage of *P* and *Mp*. The distribution of these 56 cases, in terms of recombination value with *P*, is shown in Figure 1. It is evident that there is a progressive increase in frequency as the position of *tr-Mp* approaches the *P* locus, that is, as the percentage of medium variegated plants declines. Distribution of *tr-Mp* on the two sides of *P* was not determined in these experiments. There is also a high occurrence (25 of 87 families, or 29 percent) of cases showing no recombination between *P* and *tr-Mp*. Twenty-nine of the 87 mutants yielded percentages of medium variegated segregates that did not differ significantly ($P > .05$) from 50 percent.

If at the time of the differential mitosis in which *Mp* is liberated from the *P* locus, *Mp* moved at random to a new position in the chromosome complement, only a position within 50 crossover units on either side of the *P* locus that carried the unchanged $\overline{P^{rr}Mp}$ gene would show linkage with *P*. Taking into consideration

TABLE 2

Percentage of medium variegated segregates among the testcross offspring of independent, newly arisen light variegateds

Family number	No. var. ears	Percent med. var.	Family number	No. var. ears	Percent med. var.
6D- 58	59	40.7*	N-35	9	0
63-514	94	2.1	-37	80	10.0
-519	71	19.7	-38	25	4.0
-523	125	34.4†	-40	25	48.0*
72-621	65	12.3	-42	48	56.2*
-625	60	51.7*	-44	67	0
-630	45	13.3	-47	25	0
-631	67	1.5	-49	24	0
-632	67	0	-53	35	8.6
-633	192	7.2	-59	33	42.4*
-635	162	19.1	-61	48	0
-636	70	61.1*	-65	25	0
-637	61	49.2*	-66	33	42.4*
-638	28	49.9*	-70	36	0
-639	30	53.3*	-71	37	2.7
-642	85	70.6†	-75	30	0
-643	70	31.4†	-83	29	0
-645	78	67.9†	-85	19	0
-650	95	52.6*	-89	20	45.0*
-652	95	42.1*	73-1	56	51.8*
-659	70	48.6*	-2	61	49.2*
-1160	33	54.4*	-3	98	44.9*
-1161	34	0	-4	39	17.9
-1164	28	3.6	-5	37	54.1*
-1167	15	0	-6	76	5.3
-1170	40	0	-7	51	23.5
-1172	30	13.3	-8	40	5.0
-1173	46	2.2	-9	84	42.9*
-1175	25	0	-10	47	40.4*
-1179	17	0	-11	54	0
-1183	22	0	-12	54	0
-1189	20	50.0*	-13	92	1.1
-1190	39	0	-14	25	4.0
N-4	49	0	-15	36	63.9*
-6	31	6.5	-16	44	43.2*
-9	79	57.0*	-17	36	52.8*
-10	52	5.8	-18	57	50.9*
-12	50	2.0	-19	56	17.9
-13	16	25.0	-20	33	36.4*
-16	35	51.4*	-21	75	52.0*
-27	32	0	-22	61	4.9
-28	33	0	-23	46	4.3
-30	13	7.7	-24	35	0
-32	25	0			

* Not significantly different from 50 percent ($P > .05$).

† Differs very significantly from 50 percent ($P < .01$).

FIGURE 1.—Amount of recombination between the *P* locus and transposed Modulator, as measured by the percentage of medium variegated segregates in testcross families, for 56 independently occurring mutants to light variegated.

TABLE 3

Pedigrees showing varying degrees of stability of tr-Mp position

Pedigree			Family no.	Total var.	Percent meds.
6-13-1	→ 72-143-2	→ 72-319-2	→ 72-816	53	35.8
79% lts:	7 lts:	-3	→ 72-817	36	69.4†
	2 med.-4	→ 72-318-1	→ 72-814	34	17.6
		-2	→ 72-815	47	57.4*
		→ 72-321-1	→ 72-818	46	6.5
		-6	→ 72-819	29	10.3
		→ 72-324-2	→ 72-825	44	45.4*
		→ 72-327-2	→ 72-828	47	29.8
	-7	→ 72-317-1	→ 72-813	55	20.0
		→ 72-325-1	→ 72-826	25	20.0
	-8	→ 72-322-1	→ 72-820	44	36.4
		-5	→ 72-821	61	14.7
	-11	→ 72-323-1	→ 72-823	56	3.6
		-3	→ 72-822	65	0
		-6	→ 72-824	55	3.6
		→ 72-326-1	→ 72-827	47	4.3
		→ 72-328-1	→ 72-829	51	3.9
		-2	→ 72-830	64	3.1
			Total	859	
6-184-14	→ 72-147-1	→ 72-355-1	→ 72-855	34	0
19 lts:	23 lts:	-3	→ 72-856	42	0
1 med.	1 med.	→ 72-358-3	→ 72-858	65	3.1
		→ 72-366-1	→ 72-863	47	2.1
		→ 72-377-2	→ 72-874	37	0
	-8	→ 72-357-4	→ 72-857	58	6.9
		→ 72-359-3	→ 72-859	36	2.8
	-18	→ 72-370-2	→ 72-867	43	4.6
		-3	→ 72-868	44	0
	-28	→ 72-365-1	→ 72-862	18	0
	-29	→ 72-374-1	→ 72-873	63	1.6
	-30	→ 72-363-2	→ 72-860	39	10.3
		-6	→ 72-861	18	0
	-32	→ 72-373-3	→ 72-872	45	0
	-37	→ 72-369-2	→ 72-866	64	4.7
	-42	→ 72-368-2	→ 72-865	43	2.3
	-54	→ 72-371-1	→ 72-869	119	4.2
		-2	→ 72-870	30	0
		-3	→ 72-871	53	5.7
	-56	→ 72-367-4	→ 72-864	51	2.0
	-64	→ 72-376-1	→ 72-875	17	0
		-3	→ 72-876	25	0
			Total	981	

6-196-101	→ 6-245	→ 6-304	→ 72-651	91	0
12 lts. only					
102	→ 6-262-1		→ 72-540	120	0
	15 lts-2		→ 72-541	146	0
	only -3		→ 72-542	118	0
	-4	→ Bk 952	→ 72-432	46	0
		→ 72-414-1	→ 72-683	164	0
		-2	→ 72-684	111	0
		-3	→ 72-685	104	0
			Total	900	

* Not significantly different from 50 percent ($P > .05$).

† Differs significantly from 50 percent ($P < .05$).

the differing lengths of the maize chromosomes, it was estimated that 100 cross-over units is equal to approximately 52.4 micra. This was computed by averaging the micra per 100 crossover units for chromosomes one and two, which are the longest and most uniformly marked, as given by RHOADES (1950). The total length at pachytene of the ten maize chromosomes is 552 micra. There are, therefore, an estimated 1050 crossover units on the ten chromosomes. This figure is probably a minimum. Only at a position within 100 of these 1050 units does *tr-Mp* show linkage with the *P* locus. If *tr-Mp* transposes from the *P* locus at random, only in a maximum of 9.5 percent of cases would *tr-Mp* be expected to show linkage with *P*. Of the 87 independent positions listed in Table 2, however, 56 or 64 percent show linkage with *P*.

Secondary transpositions

If the new position assumed by Modulator at the time of its primary transposition from the *P* locus were stable, then all sister families, that is, light variegated families arising from progeny of kernels from the same mutant sector on the foundation ear, should have *tr-Mp* at the same position. The pedigrees given in Table 3 show that this is not always the case. Sister families often show quite different percentages of medium variegated ears, suggesting that *tr-Mp* may continue to move after its initial transposition. Some lineages give evidence of frequent changes of *tr-Mp* position, while in others the position seems to be stable over a number of generations. Examples of these two types of pedigrees are given in Table 3. Only variegated plants, and not the colorless pericarp segregates, are shown in the pedigrees. The first pedigree given, that showing descendants of plant 6-13-1, shows positions of *tr-Mp* ranging from complete linkage with *P* to independence. At least four distinct positions linked with *P* are indicated: one between three and four units from *P*, one approximately 15 units from *P*, one about 20 units from *P*, and another about 35 units from *P*. In the second pedigree all the values could be estimates of the same position of *tr-Mp*. The third pedigree given is one in which all descendants of the sister plants 6-196-101 and -102 show no recombination between *P* and *Mp*. Pedigrees such as these suggest that there may be differences in the stability of *tr-Mp* in different positions. The examination of several such pedigrees suggested that this stability may vary according to the degree of linkage between *tr-Mp* and the variegated pericarp allele.

TABLE 4

Comparisons of linkage between variegated pericarp and tr-Mp in descendants of plants that showed various amounts of linkage between variegated pericarp and tr-Mp

Parental family		Daughter family		Parental family		Daughter families	
Percent meds.	Var. ears	Var. ears	Percent meds.	Percent meds.	Var. ears	Var. ears	Percent meds.
0	36	40	2.5	7.1	28	71	1.4
		31	0			62	3.2
		54	0				
		47	0			60	6.7
		23	0				
0	120			9.7	103	54	48.1*
		146	0			51	47.1*
		118	0				
		46	0			38	7.9
		164	0			24	4.2
0	93	111	0	13.9	72		
		104	0				
		85	0			98	3.1
		59	0			56	23.2
0	46			16.7	36		
		95	5.6				
		18	4.5				
0	51			19.6	92		
		43	4.7				
		32	3.1				
0	27			20.0	10		
		38	5.3				
		83	0				
0	37			27.2	136		
		64	0				
		44	2.3				
		29	0				
		25	8.0				
0	67	14	14.3	30.4	23		
1.0	101			34.6	26		
		47	4.3				
		35	8.6				
		80	2.5				
1.0	102			39.3	112		
		34	0				
1.7	119			40.8*	49		
		42	4.8				
		60	0				
		40	0				
1.9	54			42.3*	104		
		43	0				
		43	2.3				
		27	0				
2.7	37			45.7*	46		
		23	4.3				
		27	0				
		14	14.3				
		27	0				
3.1	64			52.5*	40		
		27	0				
		14	14.3				
		27	0				
3.6	83			53.3*	45		
		55	1.8				
		40	2.5				
6.4	47			57.4*	104		
		36	0				
				58.9*	56		
				60.9*	23		
				62.5*	40		

* Not significantly different from 50 percent ($P > .05$).

† Differs significantly from 50 percent ($P < .05$).

There were a few cases among the families grown during the course of this study in which seed from a single testcross ear was grown for classification of the progeny and also some daughter ears were testcrossed again, and the resulting progeny then grown for classification. In these groups of related families it is possible to test for successive transpositions of *Mp*. Such families are shown in Table 4, arranged according to the percent of recombination between *P* and *tr-Mp* in the stem family. In the stem families which indicated complete linkage or up to five percent recombination between *P* and *tr-Mp*, none of the daughter families show recombination values very different from that of the parent. Among the descendants of stem plants in which there was 5.1 percent to 10 percent recombination between *P* and *tr-Mp*, there seems to have been at least one move that resulted in a change from a recombination value of 9.7 percent in the parent to independence with *P* in the two daughter families. In the families in which the parent showed 10 percent to 25 percent crossing over between *P* and *tr-Mp*, moves have apparently taken place in the first family, in which the parent gave 13.9 percent recombination, as compared to 7.9 percent and 4.2 percent for the two daughter families, and in the second family in which the parent gave 16.7 percent recombinations as compared to 3.1 percent for the daughter family.

In stem families showing recombination values of 25 percent or greater (but omitting cases not significantly different from independent assortment, $P > .05$) there is evidence for at least four different moves of *tr-Mp*: at least one in the first pedigree where daughter families gave independent assortment while the parent gave only 27.2 percent crossing over; one in the second pedigree where the parent family gave 27.6 percent and the daughter showed independent assortment; one in the third pedigree—30.4 percent compared to independent assortment, and one in the fourth, 34.6 percent compared to 14.3 percent. Among the offspring of families in which *P* and *tr-Mp* assorted independently in the stem family, at least three cases are in evidence in which *tr-Mp* subsequently became linked with the *P* locus.

Moves from one position to another outside of 50 crossover units on either side of *P*, of course, cannot be detected. Short moves and moves from one side of *P* to about the same distance on the other side were not revealed by the technique used, so the estimates of the numbers of moves given in Table 4 are minimum values. Chi-square tests for independence were used where possible, but because of small plant numbers these tests were not always informative. The decisions as to when moves are indicated, therefore, are somewhat arbitrary. The results of Table 4 can be summarized as follows:

Percent crossovers <i>P-Mp</i> in parent	Total daughter families	<i>tr-Mp</i> moves indicated	Percent of moves
0	24	0	0
0.1–5	16	0	0
5.1–10	6	2	33

10 -25	5	2	40
25 up	10	4	40
indep.	13	3	23

These data suggest that *tr-Mp*'s located close to the *P* locus are less likely to move in successive generations than are *tr-Mp*'s located farther from the *P* locus. Because of the small numbers of families available for the test, however, such a relationship cannot be proved conclusively.

DISCUSSION AND CONCLUSIONS

The present data show that the sites in the genome that Modulator may occupy vary widely, thus corroborating a conclusion which McCLINTOCK (1951) had previously reached with reference to elements of this kind on the basis of her studies with Activator and Dissociation.

The criterion here used for the detection of *tr-Mp* was the modifying effect of the element on variegated pericarp. It is significant that the modifying action, as observed, is essentially the same regardless of *tr-Mp* position in the genome (cf. KEDHARNATH and BRINK 1958). The fact that variable or graded phenotypic effects are not in evidence suggests that *tr-Mp* in variegated pericarp plants does not become subliminal in any position. By the same token, the sample of *tr-Mp* positions disclosed by the technique used may be considered unbiased.

Of the 87 independently occurring transpositions tested, nearly two thirds were to sites linked with *P*, the initial position of Modulator on the short arm of chromosome 1. A computation based on total length at pachytene of all ten maize chromosomes and on the linkage map shows that if *Mp* transposed to other loci at random, then no more than one tenth of the new sites would be linked with *P*. There is a strong preference in transposition, therefore, for new sites of *Mp* in the vicinity of the old one.

The data establish the additional fact that the sites on chromosome 1 to which *Mp* is transposed are ordered in terms of recombination with *P*. The likelihood of occupation by *tr-Mp* of a particular linked site is found to be a function of the proximity of that site to *P*.

Some evidence was obtained suggesting that if transposed Modulator occupies a position close to *P* it is less likely to undergo secondary transposition than if it is located elsewhere on chromosome 1. This point requires further study. McCLINTOCK (1956b) has shown that *Ds*, which ordinarily is readily transposable (provided *Ac* also is present in the genome) may become stable in position. BRINK (1958) has described a case in which Modulator similarly became fixed at the *P* locus. There is no clue regarding the basis of such differences in transposability.

One looks in vain in the present data for evidence that the transpositions of Modulator are related to gene activation and deactivation in ways that are meaningful for development of the organism. As a component of the variegated pericarp allele, *Mp* suppresses the pigment-producing action of the *P^{rr}* gene. The latter, when present at the *P* locus alone, gives self-red pericarp and cob. Although

the point has not been established directly in the case of *Mp*, it may be presumed that the element conditions gene expression similarly at the various other loci to which it transposes. These transposition sites are diverse. The majority of them, however, lie in the same chromosome, in which they tend to be distributed in declining frequency as the crossover distance between the original *Mp* locus and the new position increases. There is no evidence that the genes over this long region are similarly ordered in terms of developmental action. One concludes, therefore, that the movements of *Mp* from one chromosome position to another are not of a kind that would be expected to impose a functional order on the gene system.

The present findings, on the other hand, suggest that mechanical factors play a predominant, although probably not an exclusive, role in the transposition of Modulator from one chromosome site to another. Further progress in the analysis of *Mp* mobility is dependent on gaining some knowledge of the processes whereby *Mp* is released from one position, transported to a new site, and then reincorporated in the chromosome.

SUMMARY

Of 87 independently occurring transpositions of Modulator (*Mp*), a component of the variegated pericarp allele at the *P* locus on chromosome 1 in maize, to other chromosome sites, 56 were found to be to positions linked with *P*. Furthermore, the closer the new site to *P*, the more likely was it to be occupied by a transposed Modulator. Evidence was obtained that Modulator also transposes to chromosomes 2, 3, 4, 5 and 9. Following a primary transposition of *Mp* from the *P* locus, the frequency of secondary transpositions varies widely from case to case.

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