

breakpoint of the reciprocal translocation T1-2b as a three marker system in a backcross mating. The location of the receptor site was estimated in 105 independent cases in which (1) a twin spot of multiple kernels was found in the pericarp, (2) the red sector was analyzed for the presence or absence of Modulator, and (3) semisterile light variegated offspring resulted from the backcross seed within the light variegated sector of the twin mutation.

Of these 105 cases, 41 showed transposed Modulator recombining at random with P, 39 were linked and distal to P, while only 18 were linked and proximal to P. The remaining 7 cases all showed Modulator linked to P but a proximal/distal relationship was not obtained. Thus, there are twice as many recovered transpositions to distal sites as to proximal sites on chromosome 1. Any sites on chromosome 1 which result in high recombination frequencies (42% or more) are tallied with the random group; thus the sites listed here as distal or proximal represent only those within a detectable linkage arc with the P locus. In addition, the proximal portion of the chromosome, three map units from P in length, was void of any receptor sites. This contrasts with the equivalent distal portion of the chromosome, which produced seventeen events. This difference in receptor site positioning adjacent to the P locus is the most striking aspect of this three-point linkage study. When transpositions occur, the condition of the immediate proximal length of chromosome is obviously in a very different state than the equivalent length of chromosome distal to the P locus.

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3. Modulator: A modifier of crossing over.

During the analysis of recombination data using P, transposed M_p and the breakpoint of T1-2b, an unexpected find was uncovered; Modulator increases the frequency of crossing over in chromosome segments adjacent to its position! Specifically, the interval T to P was found to produce recombination rates which increase when M_p is located adjacent to, but not within, the interval (see Table 3).

Table 3

The effect of Modulator's position on the frequency of recombination within a test interval on chromosome 1 marked by P and the breakpoint of T1-2b. (M_p is not within the interval.)

Group	Modulator location	Percent recombination
1	Totally absent from genome	2.30
2	Absent from <u>P</u> and <u>T</u> but present elsewhere in the genome	2.74
3	Present at <u>P</u> but not <u>T</u> and present elsewhere in the genome	3.27
4	Present at <u>P</u> and immediately adjacent to <u>T</u> only	4.18

The plant materials used in the above assessment of recombination rates were all grown in the same field, the same year, and have any genetic heterogeneity spread evenly throughout the four groupings which are compared. Group one in Table 3 represents the measured rate of recombination for a series of different red pericarp types, mutants from medium variegated, and judged to be totally void of any Modulator by use of C-Ds testers.

Group two, also a series of mutant red types from medium variegated, had been found to carry Modulator by the C-Ds tester. That means Modulator is absent from the P locus (= red phenotype) and located in an array of sites believed not too different from those mentioned in article 2 above. Their exact locations are as yet unknown, but since there are numerous different ones, there should be a good number adjacent to P but a significant number recombine at random with P.

Group three represents a collection of independently occurring light variegateds from the same medium variegated parentage as the above reds. In this group one M_p is, of course, at the P locus and the other is at sites located throughout the genome with the exception that the sites found near the T breakpoint are not included. Those cases omitted from group three are compiled as a special group four with one M_p

at P and the second, on the same chromosome strand, adjacent and proximal to the T breakpoint. When all four groups are viewed, it is obvious that the percent recombination increases when Modulator is adjacent to the test interval.

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4. Discussion of the above reports.

It is clear that transposition of Modulator from the P locus results in the mutant phenotype, red pericarp. It now appears clear that these same transpositions also cause the mutant phenotype, light variegated, to occur in equal frequency with the red mutant class. This conclusion was first advanced by Greenblatt (1968) and here tested by direct count of spots within the pericarp and again by progeny counts among the backcross offspring of a homozygous medium variegated parent. In both cases, a 1:1 ratio of red to light variegated was found. The conclusion that potential red and light variegated occur in equal frequency applies to all transpositions; there are no transpositions which would produce a red type without a concurrent light variegated type. As pointed out by Greenblatt (1968), this means that transpositions occur during that restricted period in the cell cycle when the P locus is being replicated--not before this time and not after this time.

The discovery that the proximal-distal regions adjacent to the P locus on chromosome 1 receive Modulator in a most strikingly dissimilar manner is exactly the result expected if transpositions were occurring during replication of the chromosome. As outlined in Genetics (1968), the Modulator that moves from the P locus is the one that is newly replicated, i.e., it is the one which is not from the strand that will serve as the receptor site and, in terms of semi-conservative replication, it moves from the newly forming strand to the original strand. It can only move to the original strand in those regions which are themselves in the process of replicating. As reported elsewhere, at the receptor site replication may occur a second time during the single replication of the chromosome. The interpretation of the polarity differences in site locations rests on the pattern of the