Formula and to its mathematical model. In each Specific Formula these values are reflected by individuality in the three structural units of the Manerkon: (1) In diagonalness and bend of the center base line $FC = f(M)$; (2) in successive maximum heights always directly above FC , $K_{fc} = f(M)$; and (3) in steepness of the surface, $\sigma_1 = f(M)$.

Each transverse section of the Manerkon will always show a probability curve, generally skewed, and, for the same model the total area of every such cross-section will always equal 1.000 or the probability of certainty, when measured in strips one R -unit wide.

The shape of the mathematical model reflects the genetic constitution of the subject-quality in the population which the model describes—the taller and steeper a section of the Manerkon, the more purely does that particular stretch of the population breed—the more homozygous the particular parents. On the other hand, where the Manerkonic section is relatively low, it means that for such M -region there is a wide range of offspring for each given prediction-value, and that more interacting genes, or more heterozygosity, are involved. In any case, the three coördinate scales being constant, the taller, thinner and more diagonal the Manerkon the more accurate the prediction—the more correctly is Nature's behavior pictured mathematically.

A CYTOGENETICAL STUDY OF A RECIPROCAL TRANSLOCATION IN *ZEa**

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Communicated October 20, 1933

The ten chromosomes comprising the monoploid set in *Zea* have been shown by McClintock¹ to be morphologically distinguishable from one another. Each of the ten known linkage groups in maize has been associated with a specific member of the monoploid set. For example, the genes of the $lg_1-gl_2-b-v_4$ linkage group are situated in the second longest chromosome (No. 2) while the genes of the $v_2-pr-bm_1$ linkage group are situated in the fifth longest chromosome (No. 5). This association of linkage groups with specific members of the chromosome set has been demonstrated chiefly by McClintock (largely unpublished) through her study of the different primary trisomes and the work of Burnham² and Anderson (unpublished) on reciprocal translocations in *Zea*.

The morphology of the second longest chromosome as determined by measurements at pachytene is as follows:**

DIAGRAM 1

Schematic representation of morphology of No. 2 chromosome. The position of insertion region shown by stippled region. The location of prominent knob is in the long arm. The relative ratio of the two arms is 1.0:1.4. The approximate point of breakage is shown by the vertical arrow.

and the morphology of the fifth longest chromosome is:

DIAGRAM 2

Schematic representation of morphology of No. 5 chromosome. Insertion region shown by stippled area. Knob is in long arm. Ratio of arms is 1.0:1.1. The approximate point of breakage is shown by the arrow.

A reciprocal translocation between the No. 2 and No. 5 chromosomes was found in untreated material. This reciprocal translocation led to approximately 50 per cent abortion of both ovules and pollen and was designated semi-sterile-4 since it was the fourth case of a similar nature found in *Zea*. The abortion of one-half the ovules and pollen results from the fact that the distribution of the four chromosomes in the ring of 4 is such that one-half of the gametes are deficient for a part of either the No. 2 or the No. 5 chromosome. In a previous paper³ the writer reported some linkage values obtained in a study of this translocation. The present paper will present the completed cyto-genetic study of this translocation. No attempt will be made here to review the literature dealing with translocations. This will doubtless be done when the comprehensive studies of Anderson and Burnham on translocations in *Zea* are published.

Cytological Observations.—Cytological studies at pachytene showed the points at which the translocation occurred in the two chromosomes. This is illustrated in diagrams 1 and 2 where the arrows mark the approximate points at which the breaks occurred in the two chromosomes.

DIAGRAM 3

One of the two new chromosomes formed as result of interchange between No. 2 and No. 5 at the points indicated by the arrows in diagrams 1 and 2. The insertion region is from No. 2.

DIAGRAM 4

The other new chromosome formed by the interchange. The insertion region belongs to No. 5. This new chromosome is marked by a large knob in both arms.

The two newly constituted chromosomes resulting from the translocation are shown in diagrams 3 and 4. Over twenty clear figures of the translocation complex were found at pachytene in which it was possible to identify the insertion regions, the center of the cross, i.e., the point at which the exchange of chromosome homologies occurred and to follow the four arms of the quadripartite figure. As the diagrams show the point of translocation in No. 2 occurred in the long arm but near the insertion region while the point of translocation in No. 5 was in the short arm but also close to the insertion region. The distance from the point of translocation to the insertion region in No. 2 is equal, or nearly so, to the distance from the point of translocation to the insertion in No. 5. Burnham⁴ and McClintock⁵ have shown that "sliding," which results in different positions for the point of exchange of chromosome partners in the quadripartite figure, occurred in the translocations they studied. This "sliding" or pairing of non-homologous regions makes it difficult to determine the exact positions (cytologically) of the points at which the translocation took place. This same phenomenon of "sliding" was found in the writer's translocation and often resulted in the point of exchange of partners being adjacent to the two insertion regions. The fact that the points of translocation occurred so near the insertion regions and the fact that a marked tendency was found for the center of the cross to lie close to the insertion regions, due to "sliding" or the pairing of non-homologous regions, made the cytological determination of the nature of this translocation rather difficult. The writer is greatly indebted to Dr. McClintock for her invaluable help in interpreting the cytological figures. A camera lucida drawing of the translocation complex at pachytene is shown in diagram 5.

With the occasional exception of a chain of 4 the only configuration observed at diakinesis was a ring of 4. The arrangement on the metaphase plate was of two types: (1) an open ring, or (2) a zigzag arrangement. In the first type the adjacent chromosomes pass to the same pole to give inviable combinations while in the second type of arrangement alternate chromosomes pass to the same pole to give viable combinations of two classes: (1) the two normal chromosomes and (2) the two interchanged chromosomes. The two types of arrangement on the metaphase plate probably occurred with equal frequencies but no extended counts were made.

DIAGRAM 5

A camera lucida drawing of the translocation complex at pachytene. The large knob found on the long arm of No. 2 is in a heterozygous condition while the knob on No. 5 is homozygous. The two insertion regions are shown by the stippled areas. Each line represents a single chromosome.

Genetic Studies.—Listed below are the percentages of recombination found in backcross progenies for several genes in the No. 2 linkage group with the point of interchange or translocation:

- lg_1-tr = 44.2% recombination based on a total of 2988 plants
- gl_2-tr = 31.3% recombination based on a total of 1870 plants
- $b-tr$ = 22.0% recombination based on a total of 4399 plants
- ts_1-tr = 4.5% recombination based on a total of 767 plants
- v_4-tr = 7.3% recombination based on a total of 2222 plants

Detailed data will be presented only for the backcross of individuals heterozygous for $lg_1-gl_2-b-v_4$ and the point of translocation. These data (table 1) show the point of translocation to fall between b and v_4 . Other backcross progenies involving lg_1-b and ts_1 place the point of interchange to the right of ts_1 so it is possible to state the following order: $lg_1-gl_2-b-ts_1-tr-v_4$. McClintock^{6,7} has demonstrated that lg_1 is near the left end of the short arm and that b is situated in the middle portion of the short arm of No. 2. Her studies would also suggest that the locus of v_4 lies to the right of the large knob in the long arm of No. 2 but owing to an uncertain classification for the v_4 character this location may be considered doubtful for the present. Since the break in the long arm of No. 2 occurred at a point close to the insertion region it is likely that ts_1 is in the short arm of No. 2. The v_4 gene is then the only factor of the No. 2 linkage group of 9 genes whose location is definitely in the long arm. On the basis of the available crossover data the $lg_1 gl_2 d_b b sk$ and ts_1 genes are almost certainly in the short arm while the location of fl and ba_2 is uncertain.

Since the point of translocation in chromosome 2 occurred very close to the insertion region but in the long arm the amount of crossing-over between b and the translocation should be approximately equal to the amount of crossing-over between b and the insertion region. McClintock has shown that lg_1 lies near the distal end of the short arm and that b is situated in the midportion of the short arm of chromosome 2. That is, the physical distance from lg_1 to b is of the same order as the distance from b to the insertion region. The data in table 1 give the amount of crossing-over between lg_1 and b as 35.9 per cent, while the amount of crossing-over between b and the translocation is 16.2 per cent. But the amount of crossing-over between b and the insertion region must be nearly equal to, if anything less than, the amount of crossing-over between b and the translocation. These facts seem to indicate that there is roughly twice as much crossing-over in the distal half of the short arm as there is in the proximal half. This conclusion would agree with the work of Dobzhansky on the genetic and cytological maps of the two autosomes of *Drosophila melanogaster*, who showed that the amount of crossing-over per unit of physical length was less near the insertion region than in more distal portions. However, a more precise determination of the locus of b is needed before a regional difference in crossing-over can be said to be completely established for chromosome 2 of *Zea* since a shift of the locus of b to the right of the midpoint of the short arm would vitiate the regional difference.

The recombination values between the point of interchange and four genes in the No. 5 chromosome were obtained. These values are as follows:

v_2-tr	= 50.8% recombination based on a total of 1704 plants
$pr-tr$	= 19.3% recombination based on a total of 2424 plants

bt_1-tr = 1.5% recombination based on a total of 1511 plants

bm_1-tr = 1.5% recombination based on a total of 1365 plants

Three point backcross data indicate that the order is $v_2-pr-bm_1-bt_1-tr$ although the relative order of bm_1 and bt_1 is uncertain and may be the reverse of that listed. The location of the point of interchange to the right of bm_1 and bt_1 is based in part on the frequency of double and triple cross-overs and it is possible that both bm_1 and bt_1 might be to the right of the point of breakage. However, McClintock⁷ (and unpublished) in her study of ring fragments which included the bm_1 locus believes the location of bm_1 to be in the short arm and very close to the insertion region. These facts strongly suggest that bm_1 is in the short arm of No. 5 and somewhere in the region between the insertion and the point of interchange. Since bt_1 gave the same amount of crossing-over with the break or point of interchange as did bm_1 it can be argued, but less convincingly, that bt_1 is also in the same region of the short arm as bm_1 . Strong evidence, however, was obtained through a study of $2n + 1$ individuals which arose through a 3 to 1 distribution of the four members of the ring that the order is $v_2-pr-bt-tr$.

The locus of bm_1 has been shown to be near the insertion region in the short arm of No. 5. Since there is no reduction in crossing-over between pr and bm_1 in individuals heterozygous for the translocation it can be argued that the pr and v_2 loci are situated in the long arm of No. 5. Irrespective, however, of whether or not pr and v_2 are in the long or short arm of No. 5, the data show that v_2 must occupy a more distal position than pr and that they are in the same arm. The results of the writer⁸ on chromatid crossing-over in No. 5 trisomes would also place v_2 more distant from the insertion than pr . The location of bm_1 near the insertion is also in agreement with unpublished data on chromatid crossing-over in which the frequency of exceptional bm_1 trisomes is very low.

Pseudo-Linkage of pr and bt with b .—Since viable gametes are produced only when alternate chromosomes in the ring of 4 pass to the same pole it would be expected that a factor in the No. 2 chromosome which was situated near the point of interchange would show linkage with a gene in the No. 5 chromosome whose position was also near the point of interchange in that chromosome. The intensity of this "pseudo-linkage" would depend upon the amounts of crossing-over between the two genes and the points of translocation. The factor b shows about 22% of recombination with the point of interchange in No. 2 while pr and bt_1 gave 19 and 1.5 per cent of recombination, respectively, with the point of interchange in No. 5. Therefore, cultures segregating for pr bt_1 b and the translocation should show a rather loose linkage between pr and b and a stronger linkage between bt_1 and b . In table 2 are listed such data from

backcross progenies which were segregating for the three genes and the translocation.

An inspection of table 2 discloses the striking differences in the amounts of crossing-over in mega- and microsporocytes. Unfortunately most of

TABLE 1
DATA FROM CROSS

REGIONS	$\frac{l_{g_1} gl_2 b + v_4}{l_{g_1} gl_2 b + v_4}$	$\varphi \times$	$\frac{l_{g_1} gl_2 b + v_4}{+ + + tr +}$	σ
0	$l_{g_1} gl_2 b + v_4$	=	370	
0	$+ + + tr +$	=	409	
1	$l_{g_1} + + + tr +$	=	103	
1	$+ gl_2 b + v_4$	=	99	
2	$l_{g_1} gl_2 + tr +$	=	111	
2	$+ + b + v_4$	=	116	
3	$l_{g_1} gl_2 b tr +$	=	96	
3	$+ + + + v_4$	=	97	
4	$l_{g_1} gl_2 b + +$	=	31	
4	$+ + + tr v_4$	=	21	
1-2	$l_{g_1} + b + v_4$	=	6	Region (1) = 17.3% crossing-over
1-2	$+ gl_2 + tr +$	=	10	Region (2) = 18.6% crossing-over
1-3	$l_{g_1} + + + v_4$	=	9	Region (3) = 16.2% crossing-over
1-3	$+ gl_2 b tr +$	=	4	Region (4) = 8.0% crossing-over
1-4	$l_{g_1} + + + tr v_4$	=	8	Coincidence values:
1-4	$+ gl_2 b + +$	=	18	Regions 1-2 = 0.63
2-3	$l_{g_1} gl_2 + + v_4$	=	9	Regions 1-3 = 0.32
2-3	$+ + b tr +$	=	6	Regions 1-4 = 1.18
2-4	$l_{g_1} gl_2 + tr v_4$	=	5	Regions 2-3 = 0.56
2-4	$+ + b + +$	=	15	Regions 2-4 = 1.00
3-4	$l_{g_1} gl_2 b tr v_4$	=	7	Regions 3-4 = 1.14
3-4	$+ + + + +$	=	15	
1-2-3	$l_{g_1} + b tr +$	=	5	
1-2-3	$+ gl_2 + + v_4$	=	6	
1-2-4	$l_{g_1} + b + +$	=	1	
1-2-4	$+ gl_2 + tr v_4$	=	3	
1-3-4	$l_{g_1} + + + +$	=	1	
1-3-4	$+ gl_2 b tr v_4$	=	0	
2-3-4	$l_{g_1} gl_2 + + +$	=	0	
2-3-4	$+ + b tr v_4$	=	0	
1-2-3-4	$l_{g_1} + b tr v_4$	=	0	
1-2-3-4	$+ gl_2 + + +$	=	1	
Total		=	1582	

the data on the linkage relationships in this reciprocal translocation were obtained from crosses where translocation individuals were used as the male parent. All of the recombination values reported in this paper, with the exception of table 2, are from crosses where the male parent was the heterozygote. The available data from reciprocal crosses for other

regions suggests that such a difference exists, i.e., the percentages of recombination are lower in the megasporocytes than in the microsporocytes of individuals carrying the translocation. No consistent differences were found in the reciprocal crosses of normal plants.

There is a considerable number of $2n + 1$ individuals in the progeny of a cross when plants heterozygous for the translocation are used as the female parent but these $2n + 1$ individuals cannot account for the differences in crossing-over in the reciprocal crosses.

TABLE 2

BACKCROSS DATA FROM PLANTS HETEROZYGOUS FOR THE TRANSLOCATION AND *pr* AND *bt*₁ IN NO. 5 AND *b* IN NO. 2. THE DATA LISTED UNDER THE HEADING "FEMALE" WERE OBTAINED WHEN HETEROZYGOUS INDIVIDUALS WERE USED AS THE FEMALE PARENT AND THE DATA UNDER THE HEADING "MALE" CAME FROM THE RECIPROCAL CROSS.

REGIONS		FEMALE	MALE	TOTAL
0	+ + <i>tr</i> + -	354	180	534
0	<i>pr</i> <i>bt</i> + <i>b</i> -	286	188	474
1	+ <i>bt</i> + <i>b</i> -	28	38	66
1	<i>pr</i> + <i>tr</i> + -	46	43	89
2	+ + + <i>b</i> -	1	2	3
2	<i>pr</i> <i>bt</i> <i>tr</i> + -	2	1	3
3	+ + <i>tr</i> <i>b</i> -	84	59	143
3	<i>pr</i> <i>bt</i> + + -	69	59	128
1-2	+ <i>bt</i> <i>tr</i> + -	0	1	1
1-2	<i>pr</i> + + <i>b</i> -	1	4	5
1-3	+ <i>bt</i> + + -	10	10	20
1-3	<i>pr</i> + <i>tr</i> <i>b</i> -	20	15	35
2-3	+ + + + -	2	0	2
2-3	<i>pr</i> <i>bt</i> <i>tr</i> <i>b</i> -	4	1	5
1-2-3	+ <i>bt</i> <i>tr</i> <i>b</i> -	1	0	1
1-2-3	<i>pr</i> + + + -	1	1	2
		909	602	1511
<i>pr-bt</i>		11.8%	18.6%	
<i>bt-tr</i>		1.3%	1.7%	
<i>b-tr</i>		21.0%	24.1%	
<i>pr-tr</i>		13.1%	20.3%	
<i>pr-b</i>		34.1%	44.4%	
<i>bt-b</i>		22.3%	25.8%	

As the writer pointed out in an earlier paper³ there is an absence of interference in crossing-over for two of the four arms of the quadripartite figure of the reciprocal translocation. Additional data have since been gathered which support this conclusion and the data in table 2 show the absence of interference for the *pr-tr-b* regions. It would be, of course, desirable to study interference in all four arms of the translocation but this has not yet been possible.

Dobzhansky⁹ has shown in *Drosophila* that there is a marked reduction

in crossing-over for that arm of the chromosome in which the translocation or interchange occurred. It should be possible to test for a similar reduction of crossing-over in this reciprocal translocation if the position of the point of breakage lies between two or more genes which are situated in the same arm of the chromosome. The linear order in No. 2 chromosome has been shown to be $lg_1-gl_2-b-ts_1$ -insertion region-point of translocation- v_4 . Since v_4 is the only factor in the same arm as the point of translocation an exact determination of the effect of the translocation on crossing-over is not possible. Yet the recombination values of gl_2 and b with v_4 should be different in translocation and control individuals since v_4 lies in the same arm as the break and some distance away from the insertion region. The amount of recombination between gl_2 and v_4 in translocation individuals was 32.9 per cent while the control crosses gave 42.5 per cent. More than a thousand individuals were classified in both of the two types of crosses so the difference is significant. The more critical comparison of the amount of recombination in the $b-v_4$ region was not obtained since the control data for the backcross of plants heterozygous for $lg_1 gl_2 b v_4$ were from seedling counts and an accurate classification of B and b was impossible. However, the data on the gl_2-v_4 region indicate that a reduction of crossing-over does occur in the arm of the No. 2 chromosome in which the break occurred.

Arguments have been presented for believing that v_2 *pr* bm_1 and bt_1 all lie to one side of the point of translocation in No. 5. Since bm_1 is situated in the short arm of No. 5 and with some certainty in the region between the insertion and the point of translocation, no reduction, or very little since bm_1 is near the insertion, would be expected in the percentage of recombination between *pr*- bt_1 or *pr*- bm_1 in translocation individuals as compared with the controls if *pr* was in the long arm of No. 5. No marked differences were found. The amounts of recombination found between different loci in No. 2 and No. 5 chromosomes in translocation and normal individuals are given below:

	TRANSLOCATION	CONTROL
lg_1-gl_2	21.2 per cent	21.2 per cent
gl_2-v_4	32.9 per cent	42.5 per cent
lg_1-v_4	45.7 per cent	50.2 per cent
$b-ts_1$	21.0 per cent	23.0 per cent
lg_1-b	35.0 per cent	34.0 per cent
$b-v_4$	24.2 per cent	
v_2-pr	46.3 per cent	42.0 per cent
$pr-bt_1$	18.6 per cent	17.0 per cent
	(male)	
$pr-bm_1$	30.0 per cent	29.1 per cent

* Paper No. 201 from the Department of Plant Breeding, Cornell University, Ithaca, New York.

** The ratio of the two arms of the No. 2 chromosome found in the writer's cultures is 1.0:1.4 but McClintock has found certain strains of maize where the ratio is approximately 1.0:1.2.

¹ McClintock, Barbara, *Science*, **69**, 629 (1929).

² Burnham, C. R., *Proc. Nat. Acad. Sci.*, **16**, 269-277 (1930).

³ Rhoades, M. M., *Ibid.*, **17**, 694-698 (1931).

⁴ Burnham, C. R., *Proc. Sixth Int. Cong. Genetics*, **2**, 19-20 (1932).

⁵ McClintock, Barbara, *Ibid.*, **2**, 126-128 (1932).

⁶ McClintock, Barbara, *Missouri Agr. Exp. Sta. Bull.* **163** (1931).

⁷ McClintock, Barbara, *Proc. Nat. Acad. Sci.*, **18**, 677-681 (1932).

⁸ Rhoades, M. M., *Genetics*, **18**, 535-555 (1933).

⁹ Dobzhansky, Th., *Ibid.*, **15**, 347-399 (1930).

A SECONDARY TRISOME IN MAIZE*

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Communicated November 7, 1933

Three types of trisomes have been identified in *Datura* by the cytogenetic investigations of Blakeslee, Belling and others. The primary trisomes are those in which a member of the monoploid set is represented in triplicate rather than in duplicate as is the case for the remainder of the set. Primary trisomes have been isolated in *Datura*, *Zea*, *Lycopersicum*, *Matthiola*, *Oenothera* and other plants and in *Drosophila melanogaster*. The three homologous chromosomes in a primary trisome give characteristic configurations at pachytene, diakinesis and metaphase I. A closed ring of three at diakinesis should never be found in a primary trisome since the two ends in an open V or chain of three are not homologous.

A secondary trisome differs from a primary trisome in that the extra chromosome is not a replicate of one of the members of the monoploid set but has in some way become modified so that its two ends are homologous. The conclusion that the two ends are homologous was reached from a study of the configurations at diakinesis and metaphase I (Belling and Blakeslee¹) where a ring of three or a bivalent plus a closed univalent was commonly found. No adequate studies of the prophase synapsis have ever been made in secondary trisomes so Belling's conjecture that the extra chromosome is a double half chromosome has lacked convincing support. Secondary trisomes have been found previously only in *Datura* although Philp and Huskins² may have a modified secondary in *Matthiola*.

A tertiary trisome is one in which the supernumerary chromosome is composed in part of one member of the monoploid set and in part of a different member of the monoploid set. Tertiaries have been found in