TRANSLOCATIONS IN MAIZE INVOLVING CHROMOSOME 4

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THE fourth longest chromosome in maize was first shown to carry genes in linkage group 4 by the association of semisterility due to translocation *4-8a* with the *Su su* (sugary endosperm-1) locus and by the normal ratios for *Su su* found by MCCLINTOCK (unpublished, see EMERSON *et al.* 1935) in plants trisomic for chromosome 8. The chromosome 4 translocation data summarized in the following pages amply confirm these results.

Sugary endosperms can be easily and rapidly classified, and endosperm-marked translocations in which the point of interchange shows little recombination with sugary are likely to prove valuable in a great many types of studies as ANDERSON (1952) pointed out in a case where *Y* (yellow endosperm-1) on chromosome 6 was closely linked with *su* through the use of *T4-6a*. Since, as a prerequisite to such studies, it is necessary to know the position of the interchange points relative to the gene loci under investigation, extensive studies with four genes Ts_5 (tassel seed-5) *su*, *Tu* (tunicate ear) and gl_3 (glossy seedling-3) are summarized here. EMERSON, BEADLE, and FRASER (1935) give the map positions for these genes and ANDERSON and RANDOLPH (1945) and ROMAN (1947) have shown that *su* is on the short arm to the left of the centromere. The partial linkage map thus is:

Ts_5	*su*	*Tu*	gl_3
56	71	100	111

At midprophase I of meiosis in microspore mother cells, the short arm of chromosome 4 has a mean length of 22.47 μ compared with 36.31 μ for the long arm (LONGLEY 1939). It is not uniformly stained by aceto-carmine throughout its length but appears to have a more densely staining region around the centromere, which extends distally along the arms for a third or more of the distance to the ends. Nonhomologous pairing in the heterochromatic areas around the centromere makes it difficult to assign definite exchange points for translocations. It is possible also that such a differential staining reaction may be related to the amount of recombination between two gene loci or to the amount of suppression of recombination by the interchange in heterozygous translocations.

TRANSLOCATIONS USED AND PREVIOUS INFORMATION

Linkage data have been obtained for the 33 translocations listed serially in table 1. Certain of these have been used or referred to in various previous studies and

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references to these are given in the last column of this table. The list of ANDERSON (1935) catalogs the known translocations to that time, and the papers by ANDERSON (1938, 1939) and ANDERSON and KRAMER (1954) summarize data on other chromosomes involved with 4 in interchanges. Chromosome 4 translocations have been used in such diverse studies as identifying chromosomes concerned with inheritance of such quantitative characters as smut resistance (BURNHAM and CARTLEDGE 1939; SABOE and HAYES 1941), locating centromeres on the linkage maps of maize (ANDERSON and RANDOLPH 1945), studying chromosome disjunction in interchanges with chromosome 6 (BURNHAM 1950) and selecting *su* kernels from segregating ears in early developmental stages for biochemical studies. (TEAS, CAMERON, and NEWTON 1952).

Those translocations for which no previous references are given are reported here for the first time. Their origins fall mainly into two series. The first series is derived from pollen irradiation of a *Wx Su Pr* stock by the late DR. L. J. STADLER who furnished seeds from pollinations made with the treated pollen. The second series stems from pollen irradiation of a *su wx pr* stock by DR. L. F. RANDOLPH with subsequent pollination of standard stocks carrying the normal alleles of these genes. Interchange lines were isolated from partially sterile plants grown from these seeds at the California Institute of Technology. Chromosomes involved in the interchange were identified by diakinesis tests following the method of ANDERSON (1935) or by linkage tests. Pachytene observations have since been made by LONGLEY.

PRESENTATION OF DATA

Cytological position and linkage with su

Cytological positions of the interchanges were determined from measurements made on three or four camera lucida drawings of pachytene chromosomes from plants heterozygous for the interchange. They are presented in columns two and three of table 1 as the average fraction of the distance from the centromere to the end of the arm involved. Thus, 4L.84 indicates a break far out on the long arm of 4 more than eight tenths of the distance from the centromere.

In columns four and five of table 1 are the recombination values for each interchange point with the *Susu* locus and the numbers on which these values are based. It will be noted that 19 values are below 5.0, 9 are between 5.0 and 12.0, and the remaining 5 are above 25.0. The cytological positions, however, indicate that the breaks are well distributed from 4S.79 to 4L.84. In the short arm the breaks appear to be uniformly distributed from about 4S.79 to 4S.09 but recombination values are low throughout. On the long arm, translocations in approximately the proximal third also show low recombination frequencies with *su*. Five translocations have breaks in the distal half of the long arm and these show from about 26 percent to almost 50 percent recombination. It appears, therefore, that in heterozygous translocations, suppression of recombination with *su* occurs when the interchange point is in the short arm or in the proximal third of the long arm. Further elucidation of this suppression effect is possible after considering the relative position of translocation points in the linkage map.

TABLE 1

A list of chromosome 4 translocations with cytological positions, linkage with su, *and references to previous literature*

Translocation	Position		Recombination with *su*		Reference*
	Chromosome 4	Other chromosome	No.	%	
T1-4a	4S.66	1L.49	832	3.5	A, 1935; S & H, 1941
T1-4c	4S.22	1L.33	614	2.4	
T1-4h	4L.65	1S.94	38	26.3	
T2-4a	4L.16	2L.29	361	3.3	A, 1935
T2-4b	4L.54	2L.88	215	48.8	A, 1935; S & H, 1941
T2-4c	4S.09	2L.77	1561	9.2	A, 1935; B & C, 1939; A & R, 1945
T2-4d	4L.50	2L.16	496	28.4	A, 1935; B & C, 1939
T2-4f	4L.13	2L.78	900	6.1	
T2-4g	4S.26	2L.13	997	2.7	
T2-4i	4S.37	2L.22	294	4.4	
T2-4j	4L.30	2S.19	322	1.2	
T2-4k	4L.18	2L.12	369	11.8	
T2-4l	4S.51	2L.56	345	5.8	
T2-4m	4S.46	2L.29	329	2.1	
T4-5b	4L.80	5L.70	165	43.0	
T4-5c	4S.45	5L.38	1667	1.1	B & C, 1939
T4-5d	4S.21	5L.19	385	3.4	B & C, 1939; A & R, 1945
T4-5j	4L.21	5L.40	247	5.7	
T4-5k	4S.13	5L.11	571	4.2	
T4-6a	4L.33	6L.44	1390	4.9	A, 1935; S & H, 1941; A & R, 1945; B, 1950; A, 1952
T4-6b	4S.79	6L.14	580	8.6	A, 1935; A & R, 1945; B, 1950
T4-6c	4S.29	6S.83†	707	3.7	A, 1935; A & R, 1945
T4-6e	4S.70	6L.60	592	4.9	
T4-7a	4S.27	7L.07	519	0.6	
T4-8a	4S.54	8L.23	1770	1.6	A, 1935; A, 1939
T4-8b	4S.12	8L.19	859	5.7	
T4-9a	4L.18	9L.50	1615	9.8	A, 1935; A, 1938; B & C, 1939
T4-9b	4L.84	9L.34	726	45.5	A, 1935; A, 1938
T4-9d	4L.11	9L.16	1326	3.8	
T4-9g	4S.31	9L.34	1348	3.3	
T4-10b	4L.16	10L.61	500	4.0	A, 1935; A & K, 1954
T4-10c	4S.12	10L.19	3420	1.1	A & K, 1954
T4-10e	4L.05	10L.03	783	3.3	A & K, 1954

* A = ANDERSON, A & K = ANDERSON and KRAMER, A & R = ANDERSON and RANDOLPH, B = BURNHAM, B & C = BURNHAM and CARTLEDGE, S & H = SABOE and HAYES, † = Interchange point in satellite.

Position of translocations in the linkage map

Four point backcross tests of 9 interchanges were made with *su*, *Tu*, and gl_3 and the data are presented in table 2. Additional three point tests of 5 of these and 14 additional interchanges were made with Ts_5 and *su*, or with *su* and *Tu*, and are summarized in tables 3–7. Tables 3 and 4 present tests with Ts_5 and *su* in which the breaks appear to be to the left and right of *su* respectively. Tables 5 and 6 summarize

TABLE 2

Four point backcross linkage tests with translocation points in chromosome 4

Translocation	Genotype of F1	Parental combinations	Recombinations in region							Sum
			1	2	3	1-2	1-3	2-3	1-2-3	
T1-4a	+ *su* *Tu* gl_3	18	0	11	1	1	0	0	0	67
	T + + +	20	0	16	0	0	0	0	0	
T2-4a	+ *T* + +	53	1	9	26	1	0	1	0	187
	su + *Tu* gl_3	86	1	6	3	0	0	0	0	
T2-4b	+ + + *T*	27	16	2	5	0	4	0	0	99
	su *Tu* gl_3 +	19	18	1	5	1	0	0	1	
T2-4c	+ *T* + +	37	3	21	2	0	1	0	0	130
	su + *Tu* gl_3	38	2	18	7	0	0	1	0	
T2-4d	+ + *T* +	226	85	0	6	0	9	0	0	496
	su *Tu* + gl_3	112	45	1	11	0	1	0	0	
T4-5b	+ + + *T*	62	45	3	2	0	2	0	0	165
	su *Tu* gl_3 +	27	20	0	1	3	0	0	0	
T4-5d	+ *T* + +	35	1	11	9	0	0	1	0	103
	su + *Tu* gl_3	26	1	11	8	0	0	0	0	
T4-9a	+ *T* + +	8	4	5	5	0	1	2	0	99
	su + *Tu* gl_3	46	0	6	15	2	0	5	0	
T4-9b	+ + + *T*	132	77	14	35	4	23	0	2	556
	su *Tu* gl_3 +	123	58	21	40	5	19	1	2	

results with *su* and *Tu* which again differentiate translocations with breaks to the left of *su* from those in which the break appears to be between *su* and *Tu*. Table 7 presents data on *T2-4b* which confirms the results in table 1 showing the interchange distal to *Tu*. Additional two point tests with *su* have been included in the values presented in table 1. In all of these tables, the order of presentation of reciprocal crossover classes follows that of EMERSON, BEADLE, and FRASER (1935), and where different linkage phases were used they are indicated in the table headings by number and referred to in the body of the table.

Linkage tests in homozygous translocation stocks are frequently necessary to confirm the order particularly where suppression occurs in the heterozygous translocation. Results of such tests are summarized in table 8. Only tests with genes normally in chromosome 4, and those between chromosome 4 genes and genes in the other chromosome involved which serve to clarify the order in chromosome 4 are presented.

Summary of individual translocations

An attempt has been made in table 9 to summarize recombination values from tables 1 to 7 together with additional available 2 point data and to list the translocations in their approximate order from left to right on the chromosome. The follow-

TABLE 3

Backcross progenies from 1, +T+/Ts_5 + su; *and 2,* ++su/Ts_5T+

Translocation	Genotype	Parental combinations		Recombinations in region						Sum	Percent recombination	
				1		2		1, 2			Ts_5-*T*	*T-su*
T1-4a	1	239	167	0	0	12	6	0	0	424	0.0	4.2
T2-4g	1	127	101	8	5	0	9	5	0	255	7.1	5.5
T4-6b	1	147	136	2	0	13	19	2	1	320	1.6	10.9
T4-7a	1	98	61	10	7	0	1	1	0	178	10.1	1.1
T4-7a	2	44	24	6	3	0	0	0	0	77	11.7	0.0
T4-8a	1	—	181	—	3	—	9	—	0	193	1.6	4.7
T4-8a	1	167	139	3	3	0	0	1	0	313	2.2	0.3
T4-8a	2	55	60	4	4	0	0	1	0	124	7.3	0.8

TABLE 4

Backcross progenies from 1, ++T/Ts_5su+; *2,* +su+/Ts_5+T; *and 3,* +suT/Ts_5++

Translocation	Genotype	Parental combinations		Recombinations in region						Sum	Percent recombination	
				1		2		1, 2			Ts_5-*su*	*su-T*
T2-4c	1	303	212	62	59	30	28	10	6	710	19.3	10.4
T4-5c	1	252	213	28	18	0	0	0	0	511	9.0	0.0
T4-5c	2	57	53	9	7	0	1	0	4	131	15.3	3.8
T4-5d	1	102	77	13	12	0	0	2	2	208	13.9	1.9
T4-6a	3	171	177	32	25	7	10	4	3	429	14.9	5.6
T4-8b	1	326	195	80	31	21	15	4	7	679	19.4	6.9
T4-9a	1	200	151	34	27	48	47	6	3	516	13.6	20.2
T4-9b	1	25	55	4	4	34	39	4	5	170	10.0	48.2
T4-9d	1	28	37	6	5	0	0	0	0	76	14.4	0.0
T4-9d	2	403	303	144	77	15	21	4	0	967	23.3	4.1
T4-9g	2	50	37	7	4	2	2	1	0	103	11.7	4.9
T4-10b	1	113	120	20	11	3	1	6	5	279	15.1	5.4
T4-10c	1	83	69	20	1	0	0	0	2	175	13.1	1.1

ing brief description of each translocation will serve to indicate the basis for placing each translocation in its relative position in table 9. The tables in which data for each heterozygous translocation may be found are indicated and frequent reference to the data in table 8 for the translocation homozygotes is made.

T1-4a, tables 2, 3, 5 and 8. The translocation appears to lie near *su* and probably to the left since no recombinants with Ts_5 were found. The homozygous translocation tests were inconclusive in that 42.3 percent recombination between *su* and *Tu* does not differ significantly from independence for 123 individuals.

T2-4a, tables 2, 6 and 8. The translocation is between the centromere and *Tu* on the long arm. Homozygous translocation tests showed independence for *su-Tu*. The break in 2 is in the long arm and *Tu* shows linkage with *B* on the short arm of 2 while *su* does not.

T2-4b, tables 2, 7 and 8. The break is distal to gl_3; *su* and gl_3 are linked in the homozygote.

TABLE 5

Backcross progenies from 1, +suTu/T++; *and 2,* +su+/T+Tu

Translocation	Genotype	Parental combinations		Recombinations in region						Sum	Percent recombination	
				1		2		1, 2			*T-su*	*su-Tu*
T1-4a	1	68	72	0	0	25	30	0	3	198	1.5	29.3
T2-4g	1	41	29	1	0	9	15	4	0	99	5.1	28.3
T2-4i	1	72	43	1	5	39	19	0	3	182	4.9	33.5
T4-6b	1	57	31	4	4	18	24	2	0	140	7.1	31.4
T4-6b	2	27	26	1	0	7	6	2	2	71	7.0	23.9
T4-7a	1	12	16	0	0	8	5	1	0	42	2.4	33.3
T4-8a	1	86	60	1	0	20	23	0	0	190	0.5	22.6

TABLE 6

Backcross progenies from 1, +T+/su+Tu; *2,* +++/suTTu; *and 3,* ++Tu/suT+

Translocation	Genotype	Parental combinations		Recombinations in region						Sum	Percent recombination	
				1		2		1, 2			*su-T*	*T-Tu*
T2-4a	2	68	69	2	2	20	8	2	3	174	5.2	19.0
T2-4f	1	151	144	7	3	34	38	0	1	378	2.9	19.3
T4-5c	1	143	155	6	0	58	50	0	1	413	1.7	19.1
T4-5d	1	12	42	5	0	5	8	2	0	74	9.5	20.3
T4-6a	3	106	74	7	0	17	15	0	0	219	3.2	14.6
T4-6c	1	156	144	11	2	61	75	3	3	455	4.2	31.2
T4-9a	1	185	135	1	2	31	12	2	1	369	1.6	12.5
T4-9d	1	119	98	1	5	28	28	2	2	283	3.5	21.2
T4-9g	1	170	221	7	4	47	63	4	0	516	2.9	22.1
T4-10c	1	328	382	2	3	117	117	1	1	951	0.7	24.8

TABLE 7

Backcross progeny of T2-4b *from* ++T/suTu+

Translocation	Parental combinations		Recombinations in region						Sum	Percent recombination	
			1		2		1, 2			*su-Tu*	*Tu-T*
T2-4b	34	21	15	28	10	4	2	2	116	40.5	15.5

T2-4c, tables 2, 4, and 8. This translocation is between *su* and *Tu*. In the homozygote, Ts_5 and *su* remain linked but *su* and *Tu* do not. On chromosome two the break is well out on the long arm. Linkage of *su* with v_4 but not with *Ch* on 2 and linkage of *Tu* with *Ch* in the homozygote show that the break on 4 is in the short arm between *su* and the centromere and on the long arm of 2 proximal to *Ch*, confirming the cytological placement.

T2-4d, tables 2 and 8. The break on 4 is very close to *Tu* which is confirmed by the homozygous tests.

T2-4f, tables 6 and 8. The break is between *su* and *Tu*. The cytological evidence

TABLE 8

Summary of gene recombination in backcross tests of homozygous translocation stocks

Translocation	Region	Number of individuals	Recombinations	
			Number	Percent
T1-4a	*su-Tu*	123	52	42.3
	su-gl$_3$	316	147	46.5
T2-4a	*su-Tu*	882	444	50.3
	su-B	1399	721	51.5
	Tu-B	1568	690	44.0**
T2-4b	*su-gl*$_3$	1434	619	43.2**
T2-4c	*Ts*$_5$*-su*	504	63	12.5**
	su-Tu	579	293	50.6
	su-Ch	871	431	49.5
	Tu-Ch	429	193	45.0*
	su-v$_4$	1057	401	37.9**
T2-4d	*su-gl*$_3$	235	115	48.9
	su-B	235	107	45.5
	gl$_3$*-B*	235	68	28.9**
T2-4f	*Ts*$_5$*-su*	314	50	15.9**
	su-Tu	788	414	52.5
T4-5b	*su-Tu*	373	128	34.3**
T4-5c	*Ts*$_5$*-bm*$_1$	264	14	5.3**
	su-bm$_1$	394	13	3.3**
	su-pr	394	192	48.7
	Tu-pr	584	169	28.9**
T4-5d	*Ts*$_5$*-su*	495	100	20.2**
	Ts$_5$*-a*$_2$	281	83	29.5**
	su-a$_2$	460	103	22.4**
T4-6a	*Ts*$_5$*-su*	289	36	12.5**
	su-Tu	470	236	50.2
	Ts$_5$*-pl*	289	79	27.3**
	su-Pl	1158	226	19.5**
	Tu-Pl	470	228	48.5
T4-8a	*su-Tu*	331	150	45.3
	su-ms$_8$	750	316	42.1*
	su-j	1339	557	41.6**
T4-9a	*Ts*$_5$*-wx*	262	131	50.0
	Tu-wx	491	219	44.6*
T4-10b	*Ts*$_5$*-su*	314	111	35.4**
	Ts$_5$*-g*	143	47	32.9**
	su-g	157	13	8.3**

*P < .05 **P < .01.

indicates the long arm which is supported by the independence of *su* and *v*$_4$ in the homozygous translocation.

T2-4g, tables 3 and 5. The interchange is near *su*, but the order is uncertain.

T2-4i, table 5. Near *su*, order uncertain.

T4-5b, tables 2 and 8. At the position 4L.80 the interchange is definitely distal to *gl*$_3$.

T4-5c, tables 4, 6, and 8. Data from the heterozygous interchange indicate that

TABLE 9

The approximate order from left to right of chromosome 4 translocations

Translocation	Position in 4	Recombination					
		T No.	*su* %	Ts_5 No.	*su* %	*su-Tu*	
						No.	%
Probably distal to Ts_5							
*T4-6b**	S.79	580	8.6	320	10.6	260	29.6
Probably between Ts_5 and *su*							
*T1-4a**	S.66	832	3.5	424	4.2	265	32.4
*T2-4i**	S.37	294	4.4	—	—	182	33.5
*T2-4g**	S.26	997	2.7	255	8.6	99	28.3
*T4-8a**	S.54	1770	1.6	630	4.1	190	22.6
*T4-7a**	S.27	519	0.6	255	10.6	42	33.3
*T4-10c**	S.12	3420	1.1	175	13.1	951	25.1
Between *su* and centromere							
T4-5c	S.45	1667	1.1	642	10.3	413	27.6
T4-9g	S.31	1348	3.3	103	11.6	516	23.4
T4-5d	S.21	385	3.4	208	13.9	177	24.3
*T4-6c**	S.29	707	3.7	—	—	455	32.7
T4-8b	S.12	859	5.7	679	18.0	—	—
T2-4c	S.09	1561	9.2	710	19.3	130	35.4
Between centromere and *Tu*							
T2-4a	L.16	361	3.3	—	—	361	13.9
T4-9d	L.11	1326	3.8	1043	22.6	283	21.9
T4-10b	L.16	500	4.0	279	15.1	—	—
T2-4f	L.13	900	6.1	—	—	378	21.7
T4-6a	L.33	1390	4.9	429	14.9	219	17.8
T4-9a	L.18	1615	9.8	516	13.6	468	14.7
Distal to *Tu*							
*T2-4d**	L.50	496	28.4	—	—	496	28.2
Distal to gl_2							
T4-5b	L.80	165	43.0	—	—	165	42.4
T2-4b	L.54	215	48.8	—	—	215	40.5
T4-9b	L.84	726	45.5	170	10.0	556	34.2

* Order not established with certainty.

the break is near *su* but the order is not certain. Data from the homozygote testing the Ts_5-*su* interval would be desirable but are not available. The position, however, may be definitely established in the homozygous translocation by linkage tests of Ts_5 and *su* with bm_1 on the short arm of 5 and *su* and *Tu* with *pr* on the

long arm of 5. Both Ts_5 and *su* are closely linked with bm_1; *Tu* but not *su* is linked with *pr*. The break is therefore between *su* and the centromere on the short arm of 4 and between the centromere and *pr* on the long arm of 5 confirming the cytological placement.

T4-5d, tables 2, 4, 6 and 8. The translocation is between *su* and the centromere on the short arm of 4.

T4-6a, tables 4, 6 and 8. ANDERSON (1952) has completely characterized this interchange but chromosome 4 data are included here for completeness. The break is between the centromere and *Tu* on the long arm of 4.

T4-6b, tables 3 and 5. The interchange is to the left of *su* and near Ts_5. The order with respect to Ts_5 is uncertain but possibly to the left. The cytological position at 4S.79 is farther out on the short arm than any other chromosome 4 translocation.

T4-6c, table 6. Cytological evidence places the break at 4S.29 and the genetic data place it tentatively to the right of *su*.

T4-7a, tables 3 and 5. The translocation is very close to *su* but the order is not certain and must await data on the homozygous translocation.

T4-8a, tables 3, 5, and 8. Data from the heterozygous translocation show the break to be near *su* but do not permit the order to be definitely established; nor is the recombination between *su* and *Tu* conclusive in the homozygote. In chromosome 8, ANDERSON (1939) has given the order *T*-34.2-ms_8-10.9-*j* with the break in the long arm. A three point test with the translocation homozygote gave the order *su*-42.1-ms_8-6.7-*j* for 750 plants. Additional data for the *su-j* region in the homozygote gave 41.6 percent recombination for 1339 plants. Although the linkage of *su* with ms_8 and *j* favor a break position distal to *su*, linkage of *su* with *Tu* has not been demonstrated and the order remains uncertain.

T4-8b, table 4. The order appears definitely to be Ts_5-*su*-*T* and the cytological evidence places the break at 4S.12.

T4-9a, tables 2, 4, 6 and 8. The point of interchange is between the centromere and *Tu*. Since the long arm of 9 is also involved (table 1), *Tu* is linked with *wx* in the short arm of 9 while Ts_5 is not.

T4-9b, tables 2 and 4. This is probably the rightmost of all the translocations reported. Both the position at 4L.84 and the linkage show it to be well beyond gl_3.

T4-9d, tables 4 and 6. The order is definitely Ts_5-*su*-*T*-*Tu*. Cytological examination places the break on the long arm.

T4-9g, tables 4 and 6. Data in these two tables agree in placing the translocation to the right of *su* and the position is at 4S.31.

T4-10b, tables 4 and 8. Data on the heterozygous translocation indicate only that the break is nearer *su* than Ts_5. In the homozygote, however, Ts_5 and *su* remain linked, although the recombination value 35.4 is higher than normally expected. ANDERSON and KRAMER (1954) have indicated the order *T*-*g*-*R* on chromosome 10 with the interchange in the long arm of 10. In the homozygote, both Ts_5 and *su* are linked with *g* showing that they have remained with the centromere. The break in 4 is therefore on the long arm confirming the cytological position.

T4-10c, tables 4 and 6. The interchange is very near *su* but the order cannot be established with certainty.

The nature of recombination suppression

When the translocations are arranged in their approximate linear order and grouped by region, they show a definite pattern in the suppression of recombination in chromosome 4. Such an arrangement is presented in table 9 as are the *T-su*, *Ts*$_5$-*su*, and *su-Tu* recombination percentages.

The translocations with breaks in the short arm show little or no effect on *su-Tu* recombination. Seven translocations probably to the left of *su* give 29.2 percent *su-Tu* recombination while 5 to the right of *su* give 28.7 percent. Both averages compare favorably with the standard value of 29 given by EMERSON *et al.* (1935). Similarly, breaks in the long arm appear not to affect *Ts*$_5$-*su* recombination (average of 5 translocations 13.4 percent compared to the standard value of 15. The gradation from 22.6 percent for the break nearest the centromere to 10.0 percent at the most distal point is interesting but its significance if any is not apparent.)

More important is the effect in the arm in which the break occurs. In the short arm, *T4-6b*, the only translocation which appears to be distal to *Ts*$_5$, gave 10.6 percent recombination in the *Ts*$_5$-*su* region. Five translocations which most probably lie within the *Ts*$_5$-*su* interval gave values ranging from 4.1 percent to 13.1 percent with an average of 8.1 compared with the standard value of 15. In each case there is some uncertainty regarding the order and it is possible that the higher values belong to interchanges proximal to *su*. The group of 5 translocations with breaks proximal to *su* averaged 14.6 percent recombination for *Ts*$_5$-*su*. The gradation from 10.3 percent to 19.3 percent with the higher values for breaks near the centromere may be significant.

Similarly in the long arm, 5 translocations with breaks between the centromere and *Tu* gave *su-Tu* recombinations between 13.9 and 21.9 percent and averaged 17.8 as compared with a standard value of 29. Four translocations with breaks near or distal to *Tu* gave values from 28.2 to 42.4 with 3 values significantly above the standard value.

In interpreting the nature and distribution of crossing over suppression in chromosome 4, account also must be taken of the conspicuously low recombination between *su* and the break for all translocations except those in the distal half of the long arm, i.e. near *Tu* or beyond. In general, translocations tend to reduce crossing over in the immediate vicinity of the break and to have little effect on other regions. In accord with this general observation, the chromosome 4 data would indicate that there must be a long region between *su* and the centromere in which little crossing over normally occurs. The pattern in the long arm may well be the usual one of rather low frequency near the centromere increasing in the distal half of the arm.

On this basis the observed reductions in recombination fall into the following pattern: the only translocation indicated as distal to *Ts*$_5$ shows only slight and perhaps not significant reduction in *Ts*$_5$-*su* recombination. Translocations between *Ts*$_5$ and *su* show a pronounced reduction in *Ts*$_5$-*su* recombinations. A slight reduction was recorded for translocations proximal to but near *su* while other translocations between *su* and the centromere show no reduction either in the *Ts*$_5$-*su* or the *su-Tu* region. Translocations in the long arm proximal to *Tu* show a distinct reduction in

su-Tu recombinants (29 to 17.8 percent) while the *su-T* values remain below 10 percent. The reduction thus appears to be in the more distal regions of the centromere-*Tu* region. Translocations beyond *Tu* show an abrupt rise to normal *su-Tu* values and more than 28 percent recombination between *su* and the translocation.

SUMMARY

Linkage relationships of 23 translocations involving chromosome 4 with the Ts_5, *su*, *Tu*, and gl_3 loci are reported. The recombination between the interchange point and *su* were obtained for an additional 10 translocations.

Of the 23 in which order could be determined, seven are probably to the left of *su*, six on the short arm between *su* and the centromere, six on the long arm between the centromere and *Tu*, one between *Tu* and gl_3, and three to the right of gl_3.

In heterozygous translocations, interchanges in the short arm between *su* and the centromere appear to have little effect in suppressing recombination between Ts_5 and *su*, or between *su* and *Tu* even though this region includes the *su*-centromere region. Interchanges in the centromere-*Tu* region, however, cause a definite decrease in *su-Tu* recombination. It is suggested that there is an appreciable region of undetermined length between the centromere and the *su* locus in which there is little recombination in normal stocks and that interchanges in this region therefore have little effect on recombination.

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