

TRANSLOCATIONS IN MAIZE INVOLVING CHROMOSOME 3

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INTRODUCTION

THE third longest chromosome of maize has the spindle attachment well away from the center, the long arm being twice the length of the short arm. It was shown to be associated with the $a_1 ts_4$ linkage group by means of deficiencies involving A_1 (McCLINTOCK 1931) and likewise by means of trisomics (McCLINTOCK, unpublished, cited by EMERSON, BEADLE, and FRASER 1935). This association is confirmed by the extensive series of translocation data summarized in the following pages.

ORIENTATION OF THE LINKAGE MAP

The A_1 deficiencies (McCLINTOCK 1931) involved the end of the long arm and indicated the orientation to be such that the a_1 end of the linkage map should lie toward the long arm and the cr end toward the short arm. This order has also been amply confirmed. Following the convention of orienting the maize linkage maps so that the left end corresponds to the short arm of the chromosome, the chromosome 3 map given by EMERSON, BEADLE and FRASER (1935) should be reversed to read as follows:

cr	d_1	Rg	ts_4	ba_1	na	a_1
0	18	40	47	64	75	103

TRANSLOCATIONS

The present study includes the following translocations which have been previously listed (ANDERSON 1935) with references to earlier literature: T1-3a, 1-3d, 2-3b, 2-3c, 2-3d, 3-5a, 3-5b, 3-5c, 3-6a, 3-6b, 3-7a, 3-7b, 3-8a, 3-8b, 3-9a, 3-9b, 3-10a, 3-10b, and 3-10c; also one translocation, T3-9c, described more recently (ANDERSON 1938). In addition two translocations not previously listed are included.

T2-3e was obtained from X-rayed seed (ANDERSON 1935 Lot 1). It gave two rings of four in intercrosses with T1-5b, 1-5c, 1-9a, 4-5a, 4-9b, 6-9a, and 8-10c, and a ring of six chromosomes with T1-2c, 2-4a, 2-9b, and 3-10a. The chromosomes involved have been checked by linkage tests.

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T₃-7c was obtained by DR. L. J. STADLER, Columbia, Missouri, from an X-ray treated stock. It gave two rings of four in intercrossovers with T₁-2a, 4-5a, 4-8a, and 8-9a, and a ring of six chromosomes with T₁-7a, 3-9a, 3-10a and 5-7a. The chromosomes involved have been checked also by linkage tests and by prophase cytology.

Some additional information has been published on T₃-9a, 3-9b and 3-9c (ANDERSON 1938), on T₃-8a and 3-8b (ANDERSON 1939) and on 1-3a (EMERSON 1939).

CYTOLOGY

The mid-prophase of meiosis has been observed in ten of the translocations studied. The positions of these translocations are recorded below in decimal fractions of the distance from the centromere (ANDERSON 1938). Thus 3L.1 indicates chromosome 3, long arm, one-tenth of the distance from the centromere to the end of the chromosome.

T ₁ -3a	1S.2	3L.2
T ₂ -3c	2S.6	3S.8
T ₃ -6b	3S.8	6 satellite
T ₃ -7a	3S.2	7L.25
T ₃ -7b	3S.8	7L.1
T ₃ -7c	3L.6	7L.5
T ₃ -8a	3L.6	8L.8
T ₃ -8b	3L.1	8L.2
T ₃ -9c	3L.1	9L.2
T ₃ -10a	3L.1	10L.1

The record on T₃-6b is from CLARKE and ANDERSON (1934). The remainder are from preparations made by MRS. GERTRUDE G. FRANSEN.

LINKAGE DATA

Backcross linkage tests have been made chiefly with the three gene combinations *na a*₁, *ts*₄*a*₁, and *d*₁*lg*₂. The order of four of these genes is *d*₁-*ts*₄-*na*-*a*₁, the three regions thus delimited being nearly equal in length and covering a total map distance of approximately 85 units. The data necessary to place *lg*₂ accurately in the series are not available, although two-point tests with *d*₁ and *a*₁, respectively, indicate that the gene may lie about half way between these loci. The map region which *lg*₂ serves to mark doubtless coincides in part with those of both *ts*₄ and *na*. (cf. EMERSON, BEADLE and FRASER 1935)

The data resulting from the linkage tests are presented in tables 1 to 6. The backcrosses involving *na a*₁ are given in tables 1 and 2, table 1 including the translocations to the left of *na*, table 2 those between *na* and *a*₁. Table 3 gives the backcrosses with *ts*₄*a*₁ where the order is definitely

T-*ts*₄-*a*₁ and table 4, those where the order is *ts*₄-T-*a*₁ and those where the translocation is near *ts*₄ but the order not clearly shown. Table 5

TABLE 1
Backcross progenies from $\frac{T + +}{+ na a_1}$.

TRANS- LOCATION	PARENTAL COMBINATIONS		RECOMBINATIONS						TOTAL	PERCENT RECOMBINATION	
			REGION		REGION		REGIONS			T-na	na-a ₁
			1	2	1, 2	1, 2	1, 2				
1-3a	80	63	9	14	27	25	0	6	224	12.9	25.9
2-3c	42	37	21	24	28	20	5	14	191	33.5	35.1
3-6a	71	66	31	38	51	29	11	27	324	33.0	36.4
3-7b	84	109	65	85	54	69	40	53	559	43.5	38.6
3-8a	101	98	16	10	56	43	4	9	337	11.6	33.2
3-8b	27	23	12	19	25	15	4	11	136	33.8	40.4
3-10a	58	58	15	35	30	30	16	13	255	31.0	34.9
3-10b	71	42	21	32	28	25	10	16	245	32.2	32.2

TABLE 2
Backcross progenies from $\frac{+ T +}{na + a_1}$.

TRANS- LOCATION	PARENTAL COMBINATIONS		RECOMBINATIONS						TOTAL	PERCENT RECOMBINATION	
			REGION		REGION		REGIONS			na-T	T-a ₁
			1	2	1, 2	1, 2	1, 2				
2-3d	90	55	15	11	4	6	1	0	182	14.8	6.0
2-3e	76	77	4	11	30	26	1	1	226	7.5	25.7
3-5b	147	169	8	6	40	18	1	4	393	4.8	16.0
3-5c	191	177	24	26	15	39	2	4	478	11.7	12.6

TABLE 3
Backcross progenies from $\frac{T + +}{+ ts_4 a_1}$.

TRANS- LOCATION	PARENTAL COMBINATIONS		RECOMBINATIONS						TOTAL	PERCENT RECOMBINATION	
			REGION		REGION		REGIONS			T- <i>ts</i> ₄	<i>ts</i> - <i>a</i> ₁
			1	2	1, 2	1, 2	1, 2				
1-3d	18	6	5	7	21	17	4	5	83	25.3	56.6
2-3c	103	91	19	23	104	100	22	27	489	18.6	51.7
3-7b	91	111	28	41	86	101	31	46	535	27.3	49.3

gives the backcrosses with *d*₁*lg*₂, where the order is *d*₁-T-*lg*₂ and those where the translocation is so close to *d*₁ that the order is uncertain. Table

TABLE 4

Backcross progenies from $\frac{+ T +}{ts_4 + a_1}$.

TRANS- LOCATION	PARENTAL COMBINATIONS		RECOMBINATIONS						PERCENT RECOMBINATION		
			REGION		REGION		REGIONS		TOTAL	ts_4 -T	T- a_1
			1	33	2	26	5	4			
2-3e	126	100	37	33	28	26	5	4	359	22.0	17.5
3-5b	89	79	49	36	17	28	17	13	328	35.1	22.9
3-9b	55	23	22	21	9	8	0	2	140	32.1	13.6
1-3a	100	107	2	5	111	66	4	6	401	4.2	46.6
2-3b	48	58	0	2	47	31	0	0	186	1.1	41.9
3-7a	48	41	2	4	49	52	1	3	200	5.0	52.5
3-7c	18	11	5	1	4	3	2	1	45	20.0	22.2
3-8a	239	200	9	0	123	104	2	6	683	2.5	34.4
3-9a	221	134	4	3	136	149	8	4	659	2.9	45.1
3-10a	56	81	5	6	61	60	15	4	288	10.4	48.6
3-10b	89	53	0	1	50	50	1	0	244	0.8	41.4
3-10c	181	144	2	1	85	124	0	1(?)	538	0.7	39.0

6 gives a single backcross where the order d_1 -lg-T is indicated. Some further data involving backcrosses with a single gene will be presented in the discussion of the particular translocation involved.

TABLE 5

Backcross progenies from $\frac{+ T +}{d_1 + l_{s_2}}$.

TRANS- LOCATION	PARENTAL COMBINATIONS		RECOMBINATIONS						PERCENT RECOMBINATION		
			REGION		REGION		REGIONS		TOTAL	d_1 -T	T- lg_2
			1	38	15	21	8	13			
1-3a	139	119	38	38	9	5	1	6	355	23.4	5.9
3-5a	53	41	17	17	6	5	0	0	139	24.5	7.9
3-6a	77	107	15	21	8	13	5	4	250	18.0	12.0
3-7a	119	100	30	26	23	19	9	1	327	20.2	15.9
3-8a	30	40	13	16	3	1	0	2	105	29.5	5.7
3-8b	37	32	7	7	4	2	1	1	91	17.6	8.8
3-9a	77	55	21	39	26	11	12	15	256	34.0	25.0
3-10a	80	52	10	7	20	9	0	2	180	10.6	17.2
1-3d	123	101	0	0	67	43	0	2	336	.6	33.3
2-3c	193	199	1	0	109	102	1	3	608	.8	35.4
3-7b	149	177	0	0	92	80	2	0	500	.4	34.8

TABLE 6

Backcross progeny from $\frac{+ + T}{d_1 \quad lg_2 \quad +}$.

TRANS- LOCATION	PARENTAL COMBINATIONS		RECOMBINATIONS					PERCENT RECOMBINATION			
			REGION		REGION		REGIONS 1, 2	TOTAL	d_1 - lg_2	lg_2 -T	
			1	2	1	2					
3-9b	46	46	19	28	3	6	3	0	151	33.1	7.9

SUMMARY OF INFORMATION ON INDIVIDUAL TRANSLOCATIONS

T₁-3a

For determination of linkage position, the data from tables 1, 4 and 5 may be summarized as follows:

Table 1	224 plants	T-12.9-na-25.9- a_1
Table 4	401 plants	ts_4 -4.2-T-46.6- a_1
Table 5	355 plants	d_1 -23.4-T-5.9= lg_2

The translocation lies between d_1 and the two genes lg_2 and na , closer to the latter. The order with reference to ts_4 is uncertain, but the relatively low crossing over between T and either lg_2 or na suggests as the probable order ts_4 -T- lg_2 . The observed cytological position is about L.2.

T₁-3d

In addition to the backcrosses listed in tables 3 and 5, a backcross progeny of 170 plants involving only na gave 74 crossovers, or a percentage of 43.5. These data may be summarized as follows:

Table 3	83 plants	T-25.3- ts_4 -56.6- a_1
Table 5	336 plants	d_1 -0.6-T-33.3- lg_2
na	170 plants	T-43.5-na

The translocation is very close to d_1 near the left end of the map. The order with reference to d_1 is uncertain, but the data of table 5 favor the order T- d_1 - ts_4 .

T₂-3a

This translocation is under investigation by DR. C. R. BURNHAM, Division of Agronomy and Plant Genetics, University of Minnesota, St. Paul. DR. BURNHAM kindly permits us to state that, according to his observations, the break in chromosome 3 is about midway between the centromere and the end of the long arm. Further unpublished results of genetic tests by DR. Burnham have given the following percentages of recombination: a_1 -21.6; ts_4 -15.1; na -10.4.

T2-3b

The data from table 4 show the translocation to be close to ts_4 . The crossing over shown is 1.1 percent. In view of the long map distance between ts_4 and a_1 , the data do not show whether the translocation is to the left or right of ts_4 . Preliminary cytological observations indicate a great deal of non-homologous pairing, with the possibility that an additional chromosomal disturbance has occurred at or near the point of interchange.

T2-3c

The data from tables 1, 3, and 5 together with an additional backcross involving only ts_4 are as follows:

Table 1	191 plants	T-33.5- na -35.1- a_1
Table 3	489 plants	T-18.6- ts_4 -51.7- a_1
Additional ts_4	81 plants	T-12.1- ts_4
Table 5	608 plants	d_1 -0.8-T-35.4- lg_2

The translocation is very close to d_1 , with the order uncertain. The data slightly favor the order T- d_1 - ts .

T2-3d

The backcross data from table 2 are augmented by larger backcross progenies involving the genes na and a_1 separately.

Table	182 plants	na -14.8-T-6.0- a_1
Additional na	439 plants	na -12.3-T
Additional a_1	200 plants	T-8.0- a_1

The translocation is between na and a_1 , being closer to a_1 . Of the known chromosome 3 translocations, it is nearest to the right end of the chromosome map. An average of all backcrosses gives the map values, na -13.0-T-7.1- a_1

T2-3e

The data from tables 2 and 4 are as follows:

Table 2	226 plants	na -7.5-T-25.7- a_1
Table 4	359 plants	ts_4 -22.0-T-17.5- a_1

The translocation is between na and a_1 , being closer to na . The average crossover value for the T- a_1 interval is 20.7 percent.

T3-5a

The only linkage data available are those of table 5 showing the order to be d_1 -24.5-T-7.9- lg_2 .

T₃-5b

The data from tables 2 and 4 are as follows:

Table 2	393 plants	<i>na</i> -4.8-T-16.0- <i>a</i> ₁
Table 4	328 plants	<i>ts</i> ₄ -35.1-T-22.9- <i>a</i> ₁

The translocation is between *na* and *a*₁, being closer to *na*. The average for the T-*a*₁ interval is 19.

T₃-5c

The data given in table 2, based on a backcross progeny of 478 plants, give the following order: *na*-11.7-T-12.6-*a*₁. The translocation is about midway between *na* and *a*₁.

T₃-6a

Data from tables 1 and 5 and from an additional backcross involving only *a*₁ are as follows:

Table 1	324 plants	T-33.0- <i>na</i> -36.4- <i>a</i> ₁
Table 5	250 plants	<i>d</i> ₁ -18.0-T-12.0- <i>lg</i> ₂
Additional <i>a</i> ₁	151 plants	T-45.0- <i>a</i> ₁

The translocation is in the middle portion of the section between *d*₁ and *lg*₂. The linkage relation to *ts*₄ is unknown.

T₃-6b

Cytological observations by CLARKE and ANDERSON (1934) place the interchange well out on the short arm, at about S.8. Backcrosses with *d*₁ gave only one crossover among 219 plants. The translocation is very close to *d*₁.

T₃-7a

The data from tables 4 and 5 are as follows:

Table 4	200 plants	<i>ts</i> ₄ -5.0-T-52.5- <i>a</i> ₁
Table 5	327 plants	<i>d</i> ₁ -20.2-T-15.9- <i>lg</i> ₂

The translocation is in the mid-region between *d*₁ and *lg*₂, a short distance from *ts*₄. The direction from *ts*₄ is uncertain.

T₃-7b

The data from tables 1, 3 and 5 are as follows:

Table 1	559 plants	T-43.5- <i>na</i> -38.6- <i>a</i> ₁
Table 3	535 plants	T-27.3- <i>ts</i> ₄ -49.3- <i>a</i> ₁
Table 5	500 plants	<i>d</i> ₁ -0.4-T-43.8- <i>lg</i> ₂

The translocation is very close to *d*₁. While the order is uncertain, the data from table 5 slightly favor T-*d*₁-*ts*₄. Cytological observation places the interchange well out on the short arm, at about S.8.

T₃-7c

The small backcross family of 45 plants listed in table 4 indicates a position midway between *ts*₄ and *a*₁. The cytological position of the interchange is about halfway, or slightly more than half way, out on the long arm, (L.5 to L.6).

T₃-8a

Data from tables 1, 4 and 5 are as follows:

Table 1	337 plants	T-11.6-na-33.2- <i>a</i> ₁
Table 4	683 plants	<i>ts</i> ₄ -2.5-T-34.4- <i>a</i> ₁
Table 5	105 plants	<i>d</i> ₁ -29.5-T-5.7- <i>lg</i> ₂

The translocation is rather close to *ts*₄. The order with reference to *ts*₄ is uncertain, but the relatively low crossing over with *na* and *lg*₂ suggests the order *ts*₄-T-*na*. The cytological position is about L.6. The cytological preparations were among the earliest ones made, and are less reliable than those made more recently.

T₃-8b

In addition to data from tables 1 and 5, there are available some data on backcrosses with *ts*₄ and with *lg*₂.

Table 1	136 plants	T-33.8-na-40.4- <i>a</i> ₁
Table 5	91 plants	<i>d</i> ₁ -17.6-T-8.8- <i>lg</i> ₂
Additional <i>lg</i> ₂	199 plants	T-17.6- <i>lg</i> ₂
Additional <i>ts</i> ₄	264 plants	no crossovers

The translocation is very close to *ts*₄. The cytological position of the break is in the long arm, not far from the centromere (about L.1).

T₃-9a

Data from tables 4 and 5 are as follows:

Table 4	659 plants	<i>ts</i> ₄ -2.9-T-45.1- <i>a</i> ₁
Table 5	256 plants	<i>d</i> ₁ -34.0-T-25.0- <i>lg</i> ₂

The translocation is near *ts*₄ but the order with reference to this locus is uncertain.

T₃-9b

Besides the data in tables 4 and 6, there is one backcross progeny involving only *a*₁.

Table 4	140 plants	<i>ts</i> ₄ -32.1-T-13.6- <i>a</i> ₁
Table 6	151 plants	<i>d</i> ₁ -33.1- <i>lg</i> ₂ -7.9-T
Additional <i>a</i> ₁	155 plants	T-24.5- <i>a</i> ₁

The translocation is probably to the right of *lg*₂ in the direction of *a*₁, but the data are not conclusive. A three-point test with *na a*₁ or *lg*_{2 a₁ is needed.}

T_{3-9c}

No backcross data have as yet been obtained. A few small F₂ cultures from a cross with *na a*₁ showed a considerable amount of crossing over between T and *na*, indicating a position for the translocation well to the left of *na*. This is in agreement with the cytological placement of the break at L.1.

T_{3-10a}

Data are available from tables 1, 4 and 5 from an additional backcross involving only *d*₁.

Table 1	255 plants	T-31.0- <i>na</i> -34.9- <i>a</i> ₁
Table 4	288 plants	<i>ts</i> ₄ -10.4-T-48.6- <i>a</i> ₁
Table 5	180 plants	<i>d</i> ₁ -10.6-T-17.2- <i>lg</i> ₂
Additional <i>d</i> ₁	71 plants	<i>d</i> ₁ -12.7-T

The data are somewhat conflicting, but indicate the position of the translocation as nearest to *ts*₄. The data from table 4 favor *d*₁-T-*ts*₄ as the most probable order. The cytological position of the break is recorded as L.1 to L.2.

T_{3-10b}

Data from tables 1 and 4 are as follows:

Table 1	245 plants	T-32.2- <i>na</i> -32.2- <i>a</i> ₁
Table 4	244 plants	<i>ts</i> ₄ -0.8-T-41.1- <i>a</i> ₁

The translocation is very close to *ts*₄.

T_{3-10c}

The backcross data on 538 plants listed in table 4 show 0.7 percent crossing over with *ts*₄ and 39.0 percent with *a*₁.

THE DISTRIBUTION OF THE TRANSLOCATIONS ON THE CHROMOSOME

The translocations involving chromosome 3 fall into three groups on the basis of present data: (1) a group of four at the left end rather closely linked to *d*₁ (2) a group of five or six at the right end in the vicinity of *na* and *a*₁ and (3) the remaining translocations in the whole middle region of the chromosome map which show fairly close linkage with *ts*₄.

The group of translocations at the left end may be tabulated as follows:

	Cytological position	Crossing over with <i>d</i> ₁	Crossing over with <i>ts</i> ₄
T _{3-6b}	S.8	0.5	
3-7b	S.8	0.4	27.3
2-3c	S.8	0.8	17.7
1-3d		0.6	25.3

In each of these the crossing over with d_1 is less than one percent. The three which have been studied cytologically have the interchange well out toward the end of the short arm of the chromosome.

The group at the right end may be tabulated in similar fashion:

T ₃ -7c	<i>ts</i> ₄ -20.0-T-22.2- <i>a</i> ₁
3-9b	<i>lg</i> ₂ - 7.9-T-18.0- <i>a</i> ₁
3-5b	<i>na</i> - 4.8-T-19.1- <i>a</i> ₁
2-3e	<i>na</i> - 7.5-T-20.7- <i>a</i> ₁
3-5c	<i>na</i> -11.7-T-12.6- <i>a</i> ₁
2-3d	<i>na</i> -13.0-T- 7.1- <i>a</i> ₁

Only one of these, T₃-7c, has been studied cytologically, its position being about L.6. But here the linkage data are so few that they can only be taken as indicating the position of the translocation in the general neighborhood of *lg*₂ and *na*.

The remaining translocations form a group rather closely linked to *ts*₄. The direction from *ts*₄ in each case is uncertain due to the long distance between the two genes *ts*₄ and *a*₁ used in the tests. Those tested with d_1lg_2 lie within this long interval, well away from either gene. Most of the translocations appear to partially suppress crossing over. These translocations are listed in table 7, arranged roughly in the order of the observed crossing over with d_1 and *lg*₂, where such data are available.

TABLE 7
*Translocations closely linked to ts*₄.

TRANS- LOCATION	CYTOLOGICAL POSITION	PERCENT CROSSING OVER WITH			
		d_1	<i>lg</i> ₂	<i>ts</i> ₄	<i>na</i>
T ₃ -9a		34.0	25.0	2.9	
3-7a	S.2	20.2	15.9	5.0	
3-8b	L.1	17.6	14.8	0	33.8
3-9c	L.1				
3-10a	L.1	11.2	17.2	10.4	31.0
2-3b				1.1	
3-10b				0.8	32.2
3-10c				0.7	
3-6a		18.0	12.0		33.0
3-5a		24.5	7.9		
1-3a	L.2	23.4	5.9	4.2	12.9
3-8a	L.6	29.5	5.7	2.5	11.6

The apparent grouping of more than half of the translocations close to *ts*₄ is probably due in part to a partial suppression of crossing over in at least some of the translocations. It is also suggested that there may be a

considerable part of the middle portion of the chromosome in which relatively little crossing over takes place.

The centromere cannot yet be located with any certainty, except that its position must lie somewhere in the long region between d_1 on the left and the two genes lg_2 and na on the right. The most probable location is near ts_4 . Closer determination must await further cytological study and linkage tests with homozygous translocations.

SUMMARY

Studies are reported on 21 translocations in maize involving chromosome 3. The translocations are distributed from the neighborhood of d_1 , well out on the short arm, almost to a_1 in the distal part of the long arm.

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