

TRANSLOCATIONS IN MAIZE INVOLVING CHROMOSOME 9

E. G. ANDERSON

California Institute of Technology, Pasadena, California

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INTRODUCTION

THE *C wx* linkage group associated with chromosome 9 was one of the first to be established in maize. This was largely due to the excellence of the two genes *C* and *wx* as working tools. EMERSON, BEADLE and FRASER (1935) list 28 genes in this group. Nearly all of these are to the left of *wx* or within 10 or 15 units to the right. McCLINTOCK (1930, 1931), CREIGHTON and McCLINTOCK (1931), CREIGHTON (1934) and BURNHAM (1930, 1934a, b) have shown that the gene *yg₂* is near the end of the short arm of chromosome 9 and *wx* nearer the spindle attachment but still on the short arm. *Virescent₁* (*v₁*) is probably on the long arm not far from the spindle attachment (BEADLE 1932, BURNHAM 1934b). The greater portion of the long arm is conspicuous by its lack of definitely known genes. This lack of known genes may be largely due to the difficulty of detecting genes in the distal part of the long arm by means of ordinary linkage tests with such genes as *C*, *sh* and *wx*. Or it may be that such regions are redundant sections of chromosome materials which are also represented elsewhere in the chromosome complement.

Chromosomal interchanges or reciprocal translocations are excellent tools for the exploration of portions of chromosomes where no known genes are available. For most cases it is only necessary to cross any new or unplaced gene with the appropriate translocation stock, backcross with the new gene if recessive or with a normal stock if dominant. Classification of the gene character under consideration and semisterility will give a direct linkage test with a known point on the chromosome.

The chromosome 9 translocations studied by the writer have all been on the long arm, mostly in the region beyond the present known genes. They do not add appreciably to our knowledge of the region covered by the present linkage maps, but do furnish excellent means for the placement and mapping of genes in the extensive region of the long arm where no genes are as yet available.

PREVIOUS DATA ON TRANSLOCATIONS INVOLVING CHROMOSOME 9

T8-9a (BURNHAM 1930, 1934b; McCLINTOCK 1930, 1931; CREIGHTON and McCLINTOCK 1931; BEADLE 1932). The interchange on chromosome 9 on the long arm .4 of distance out from spindle attachment. Linkage order *C-wx-T* with 13.7 percent of crossing over with *waxy*.

- T5-9a (BURNHAM 1934a). Interchange in proximal part of the short arm of chromosome 9. Linkage order *sh-wx-T* with about two percent of crossing over with waxy. Much non-homologous pairing and much suppression of crossing over.
- T6-9a (ANDERSON 1934, McCLINTOCK 1934). Interchange about one-third the way out on the long arm of chromosome 9. Linkage order *C-wx-T* with 11.6 percent of crossing over with waxy.

TRANSLOCATIONS INCLUDED IN THE PRESENT STUDY

In the present paper, data are presented on the following translocations which are included in the writer's published list (ANDERSON, 1935); T 1-9a, b, c, 2-9a, b, 3-9a, b, 4-9a, b, 6-9a, b, and 8-9b. In addition two others are included which will be designated T3-9c and T9-10b. Both were from the writer's X-rayed material (ANDERSON 1935, Lot 1, sixty minute treatment, and Lot 2, fifty minute treatment, respectively). The chromosomes involved were determined by diakinesis observations of intercrossovers with known translocations. T3-9c gave two rings of four in crosses with T 1-2a, T 1-7a, T 4-8a, T 5-7a and T 4-5a, and a ring of six with T 8-9a and T 2-3a. T 9-10b gave two rings of four with T 1-7a, T 4-8a, T 4-5a, and T 2-3a, and a ring of six with T 3-9a and T 3-10a. These determinations of chromosomes involved have been checked by cytological observation at mid-prophase and by linkage tests.

No data are presented on T 9-10a as this translocation involves problems connected with the survival of unbalanced gametes and will be reported as a separate paper.

LINKAGE DATA

Since most of the linkage tests with genes from chromosome 9 were made involving the same genes in the same linkage order, the summarized data have been combined in a few tables. The individual cultures have been fairly consistent with the exception of T 4-9a and T 6-9a which are presented in more detail. Except for T 6-9a, backcrosses using the F_1 as male or female have given similar results and are combined in the tables. The arrangement of data in the tables is like that in the linkage summary of EMERSON, BEADLE and FRASER (1935).

Backcross data involving various translocations with the two genes *C* and *wx* are presented in table 1. Data similarly involving the three genes *C*, *sh* and *wx* are presented in table 2. Additional data involving only *wx* are given in table 3 while table 4 gives data involving the genes *C* and *sh* with T 8-9b. In several of the backcross cultures there were large discrepancies between several of the contrary classes, due partly to lower viability of *sh* and *wx*, but chiefly to the presence of yg_2 and one other weak

TABLE 1
Backcross progenies from combinations $\frac{C+T}{+wx+}$

	PARENTAL COMBINATIONS		RECOMBINATIONS						TOTAL	PERCENT RECOMBINATION COINCIDENCE		
			REGION 1		REGION 2		REGIONS 1, 2			1 <i>c-wx</i>	2 <i>wx-T</i>	I, 2
T 1- 9a	154	130	50	45	36	7	1	4	427	23.4	11.2	.44
T 1- 9b	99	68	34	30	76	56	14	15	392	23.7	41.1	.76
T 1- 9c	74	71	24	38	22	1	6	1	237	29.1	12.7	.80
T 2- 9a	42	47	15	19	27	20	9	12	191	28.8	35.6	1.07
T 2- 9b	219	225	54	83	22	20	2	3	628	22.6	7.5	.47
3- 9a	116	55	29	8	5	2	—	—	215	17.2	3.3	—
3- 9b	127	148	45	50	10	11	3	3	397	25.4	6.8	.87
3- 9c	65	65	15	25	14	2	—	1	187	21.9	9.1	.27
4- 9a	76	68	18	43	29	40	9	14	297	28.3	31.0	.88
4- 9a	134	123	46	51	24	16	1	5	400	25.7	11.5	.51
6- 9b	238	220	41	62	15	4	—	3	583	18.2	3.8	.75
8- 9b	31	31	9	11	25	14	4	6	131	22.9	37.4	.89
9-10b	175	126	67	77	14	12	1	—	472	30.7	5.7	.12

chlorophyll gene in some of the *c wx* stocks used. Under somewhat unfavorable weather conditions these proved practically lethal. While theoretically a lethal gene should not alter the linkage percentages, data in-

TABLE 2
Backcross progenies from combinations $\frac{C+ +T}{+sh wx+}$

	PARENTAL COMBINATIONS		RECOMBINATIONS							TOTAL				
			REGION 1	REGION 2	REGION 3	1 AND 2	1 AND 3	2 AND 3	1, 2 AND 3					
T 1-9b	132	69	2	7	25	25	66	49	2	2	9	8	1	397
1-9c	145	41	3	3	28	29	24	5	1		1	3		283
2-9a	42	34	3	1	13	15	19	6			3	3	—	139
4-9a	57	21	1	2	17	15	8	2	1		2	3		129
4-9b	68	78	6	1	19	14	1	4	1		1			193

TABLE 3
Backcross progenies from combinations $\frac{+T}{wx+}$

	PARENTAL COMBINATIONS		RECOMBINATIONS		TOTAL	PERCENT RECOMBINATIONS
2-9a	63	56	31	25	175	32.0
3-9a	202	176	9	6	393	3.8
3-9c	67	66	6	2	141	5.7

TABLE 4
Backcross progeny from $\frac{C+T}{+wx+}$

	PARENTAL COMBINATIONS		RECOMBINATIONS					TOTAL	PERCENT RECOMBINATION		
			REGION 1	REGION 2	REGIONS 1, 2		<i>c-sh</i>		<i>sh-T</i>		
T 809b	65	55	1	3	28	34	2	1	189	3.7	34.4

volving a lethal gene are not entirely trustworthy for accurate determinations. But for the approximations required in the present work, the data are probably accurate enough.

The T 4-9a progenies fall into two sharply different groups. Three cultures from a single plant, 11-315-2, gave 10.2, 12.2, and 11.6 percent crossing over for the *wx-T* interval. Two cultures from sibs of this plant gave 27.1 and 34.9 percent for the same region. A closely related plant gave 27.6 percent. The two groups of data have been summarized separately. Cytological observations of one plant at mid-prophase of meiosis has shown the interchange of chromosomes about four fifths the way out on the long arm of 9 and very near the spindle attachment on 4. This position would give an expectation of loose linkage corresponding to the higher crossover value. The low value obtained in cultures from 11-315-2 might be due to the presence of some other chromosomal alteration such as the short inversion about the spindle attachment of chromosome 4 which is known to be present in some stocks (McCLINTOCK 1933).

Some further data have been obtained on T 6-9a. Two sister F₁ plants were backcrossed reciprocally with a *c wx* stock. The data are given in table 5. With such small numbers of plants involved, not much reliance can be placed on these data. There is a marked difference in the crossover values when the plants are used as female or male, but the difference is opposite to that previously found for the T -Y -*Pl* region of chromosome 6 (ANDERSON 1934). Obviously the crossing-over behavior of T 6-9a needs to be checked more carefully.

TABLE 5
Reciprocal backcrosses of T 6-9a. Parental formula $\frac{C+T}{+wx+}$.

F ₁ PARENT USED AS	F ₁	PARENTAL COMBINATIONS		RECOMBINATIONS						TOTALS	PERCENT CROSSING OVER	
				REGION 1		REGION 2		REGIONS 1, 2			C-wx	wx-T
II-318-1	♀	18	20	8	9	6	7	2	0	70	27.1	21.4
	♂	108	107	26	45	9	2	1	2	300	24.7	4.7
II-318-5	♀	51	52	35	24	4	9	5	3	183	36.6	11.5
	♂	78	17	12	12	3	2	2	1	127	21.3	6.3

CYTOLOGY

Cytological examinations have been made of aceto-carmin preparations at mid-prophase of meiosis. Measurements and estimates of position of the interchange of chromosomes have been made from camera lucida tracings of the clearest figures. The position of the interchange is recorded in tenths of the distance from the spindle attachment to the end of the arm. Thus 9 L.4 indicates chromosome 9 long arm four-tenths of distance from the spindle attachment. In general these placements are probably reliable to about .1 or .2 of the length of the arm. Those near the end of the chromosome are somewhat less reliable. In some cases, notably T 5-9a (BURNHAM 1934a) and T 6-9b, there is much non-homologous pairing (McCLINTOCK 1933), which makes it difficult to determine the normal position of the interchange.

The three translocations T 8-9a, T6-9a, and T 5-9a have been described. The following have been examined cytologically:

T 1-9b	1 L .6	9 L .5
T 1-9c	1 S .6	9 L .2+
T 2-9a	2 S .7	9 L .6+
T 2-9b	2 S .1	9 L .2
T 3-9a	—	9 L .1+
T 3-9c	3 L .1	9 L .2
T 4-9a	4 L .1	9 L .8
T 4-9b	4 ^F L .6	9 ^F L .2
T 8-9b	8 ^F S .2	9 ^F L .8
T 9-10b	9 L .3	10 near s.a.

T 1-9a and T 3-9b have not been studied. T 6-9b shows much non-homologous pairing, but seems to have the interchange in the proximal part of the long arm of 9.

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RELATION OF POSITION OF INTERCHANGE TO LINKAGE WITH WAXY

TABLE 6

Comparison of position of interchange with map distance from waxy.

	CYTOLOGICAL POSITION	PERCENT CROSSING OVER FROM <i>wx</i>	NUMBER OF PLANTS IN LINKAGE TESTS
T 5-9a	S .1	2.0	(BURNHAM 1934a)
3-9a	L .1+	3.6	608
4-9b	L .2	3.1	193
6-9b		3.8	583
3-9b		6.8	397
2-9b	L .2	7.5	628
3-9c	L .2	7.6	328
1-9c	L .2+	12.1	520
9-10b	L .3	5.7	472
6-9a	L .3	9.4	955
1-9a		11.2	427
8-9a	L .4	13.7	(BURNHAM 1934b)
1-9b	L .5	37.7	789
2-9a	L .6+	30.7	505
4-9a	L .8	31.0	297
		11.5	529
8-9b	L .8	37.4	131

Table 6 gives a list of the interchanges involving chromosome 9 arranged in approximate order of their position in the chromosome and of their crossover distance from *waxy*. The first column gives the observed position in chromosome 9. The second column gives the percent of crossing over from *waxy*. The third column gives the total number of backcross plants on which the crossover percentages are based, summarized from the preceding tables. The correlation between the cytological observations and the percentages of crossing over is very close, considering the probable amount of error in the cytological placements. The loose linkages shown by T 1-9b, T 2-9a, T 4-9a, and T 8-9b probably represent longer map distances, which can be studied more effectively when one or more helpful genes are found in the distal part of chromosome 9.

SUMMARY

Data are presented on linkage relations with *waxy* for fourteen translocations involving the long arm of chromosome 9.

The amount of crossing over with *waxy* is closely correlated with the cytological position of the interchange (table 6).

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