TRANSLOCATIONS IN MAIZE INVOLVING CHROMOSOME 6

E. G. ANDERSON, H. H. KRAMER, AND A. E. LONGLEY

Kerckhoff Laboratories of Biology, California Institute of Technology, Pasadena[1], *Purdue University, Lafayette, Indiana*[2], *and Field Crops Research Branch, U. S. Department of Agriculture*

Received December 13, 1954

CHROMOSOME 6 of maize may be characterized by the presence of the nucleolus organizer region (and the small portion beyond, known as the satellite). Its association with the *Y-Pl* (yellow endosperm-1, purple plant color) linkage group was established by MCCLINTOCK (1931) by a study of trisomic plants and by means of a deficiency in the long arm which showed the orientation to be nucleolus-*Y-Pl*. BRINK and COOPER (1932) presented linkage data for *T1-6a* (semisterile-5) and established the order nucleolus-*Y-Pl-T* for this translocation.

The presence of *Y* and the nucleolus organizer region has made translocations involving chromosome 6 particularly valuable as tools in a number of important studies. Evidence was provided by *T1-6b* (BURNHAM 1932) that centromere disjunction is reductional at anaphase I of meiosis. BURNHAM (1949, 1950) used the nucleolus organizer to show that the frequency of disjunction types in translocations is closely related to lengths of interstitial segments. The close linkage of *Y* with *su* (sugary endosperm-1) on chromosome 4 in *T4-6a* (ANDERSON 1952) and the early appearance of yellow color was used by TEAS *et al.* (1952) to separate developing sugary and starchy kernels on segregating ears for a comparative study of tryptophan, niacin, indole acetic acid, and carbohydrates during their ontogeny.

In studies illustrated by the foregoing examples as well as studies to localize sections of chromosomes associated with such characters as smut resistance (BURNHAM and CARTLEDGE 1939), leaf firing (SABOE and HAYES 1941), and resistance to attack by the European corn borer (IBRAHIM 1954), it is important to know the positions of the breaks and their linkage relations with genes whose relative positions on the linkage maps are known.

The present paper summarizes the available information for those translocations involving chromosome 6 to which permanent numbers have been assigned.

CYTOLOGICAL POSITIONS AND PREVIOUS INFORMATION

Forty-six translocations involving chromosome 6 are listed serially in table 1. Cytological re-examinations of the break positions were made from material grown in 1954 and the positions are given in this table as the fraction of the distance from the centromere to the end of the arm involved. Thus 6L.82 indicates a break far out on the long arm of chromosome 6 while 6S.09 indicates a break near the centromere on the short arm. These positions supplant those which may have been given in earlier publications. References are given in this table to the principal papers in which the translocations previously have been studied or used. Attention should be

[1] This work was supported by funds supplied by the Atomic Energy Commission through the Office of Naval Research. U.S.N., Contract N6-onr-244, Task order 5, Project NR-164-340.

[2] Journal paper No. 828 of the Purdue University Agricultural Experiment Station.

TABLE 1

List of translocations involving chromosome 6, cytological positions, and references to previous studies

Translocation	Cytological positions		Reference*	Translocation	Cytological positions		Reference*
T1-6a	1L.21	6L.59	1, 9, 11, 12	*T5-6a*	5L.32	6L.47	1, 11
T1-6b†	1L.25	6S[s]	1, 10, 11, 13	*T5-6b*	5L.71	6L.29	11
T1-6c	1S.17	6L.39	4, 11	*T5-6c*	5L.81	6S.11	11
T1-6d	1L.10	6S.71[o]	11, 15	*T5-6e*	5L.20	6L.63	
T1-6e	1S.37	6L.40		*T5-6f*	5S.29	6S.70[o]	
T1-6f	1L.35	6L.45					
T1-6g	1L.16	6L.84		*T6-7a*	6L.74	7L.61	
T1-6h	1L.05	6L.16		*T6-8a*	6L.41	8L.73	1, 3, 11, 12
				T6-8b	6L.73	8S.72	
T2-6a	2S.51	6S.09	1, 11, 12	*T6-8c*	6L.29	8L.50	
T2-6b	2S.69	6L.49	1, 14	*T6-8d*	6L.51	8L.78	11
T2-6c	2L.32	6L.20	1, 11, 14	*T6-9a*	6S.79[o]	9L.40	1, 2, 13, 14, 16
T2-6d	2L.41	6L.45	1, 11	*T6-9b*	6L.13	9S.42	1, 2, 11
T2-6e	2L.28	6L.22	1	*T6-9c*	6L.17	9L.20	11
T2-6f	2L.78	6L.87		*T6-9d*	6S.81[o]	9L.86	14
				T6-9e	6L.17	9L.22	14
T3-6a	3L.08	6L.26	1, 6, 11	*T6-10a*	6L.68	10L.19	1, 7, 11, 12, 14
T3-6b	3S.70	6S.77[s]	1, 6, 11	*T6-10b*	6L.18	10L.21	7, 11
T3-6c	3S.56	6L.54	11, 14, 15	*T6-10c*	6L.51	10S.40	
T3-6d	3L.28	6L.83		*T6-10d*	6L.15	10L.06	
				T6-10e	6L.15	10S.15	
T4-6a	4L.33	6L.44	1, 5, 8, 11, 16	*T6-10f*	6S.92[s]	10S.30	
T4-6b	4S.79	6L.14	1, 8, 11	*T6-10g*	6L.86	10L.19	
T4-6c	4S.29	6S.83[s]	1, 8	*T6-10h*	6L.48	10L.86	
T4-6d	4L.46	6L.56	15				
T4-6e	4S.70	6L.60	8, 14				

* 1, 2, 3, 4, 5, ANDERSON 1935, 38, 39, 41, 52; 6, ANDERSON and BRINK 1940; 7, ANDERSON and KRAMER 1954; 8, ANDERSON, KRAMER, and LONGLEY 1955; 9, BRINK and COOPER 1932; 10, 11, BURNHAM 1932, 50; 12, BURNHAM and CARTLEDGE 1939; 13, EMERSON, BEADLE, and FRASER 1935; 14, IBRAHIM 1954; 15, ROBERTS 1942; 16, SABOE and HAYES 1941.

† Position by BURNHAM 1932.

[s] Satellite. [o] Nucleolus organizer.

called specifically to those translocations reported under different designations than the permanent numbers assigned here. These are *T1-6a*, reported first as semisterile-5 (BRINK and COOPER 1932) *T1-6b*, reported as a low sterile by BURNHAM (1932), *6-8d*, previously *6-8D-1* and *6-9c*, previously *6-9A66* (BURNHAM 1950) and three reported by ROBERTS (1942), namely, *T1-6d* (*Conn.R28*), *3-6c* (*Conn.R34*), *4-6d* (*Conn.R43*). Certain translocations are reported here for the first time. They were obtained by X-ray treatment as described by ANDERSON *et al.* (1955).

LINKAGE DATA

Linkage tests were made with the genes *Y*, *Pl*, *sm* (salmon silks), and *py* (pigmy plant). The position of these four genes on the linkage map given by RHOADES (1950) is

Y	*Pl*	*sm*	*py*
13	44	54	64

.

TABLE 2

Three-point linkage tests of translocations involving chromosome 6

Translocation	Genotypic group	Parental		Recombination in region 1		Recombination in region 2		Recombination in region 1, 2		Total	Percent recombination Region 1	Percent recombination Region 2
Genotypic groups 1, *Y + Pl/ + T +*; and 2, *Y ++ / + T Pl*												
T1-6c	1	90	86	0	2	13	9	0	0	200	1.0	11.0
T3-6a	2	66	47	1	7	3	0	2	0	126	7.9	4.0
T4-6c	1	50	67	0	0	14	21	0	0	152	0.0	23.0
T6-8a	1	45	33	7	4	0	0	0	0	99	11.1	0.0
	1	47	63	7	6	0	15	1	0	139	10.1	11.5
T6-9b	1	144	180	0	1	6	14	0	0	345	0.3	5.8
	1	49	107	1	3	6	2	1	1	170	3.5	5.9
Genotypic groups 3, *+ Pl sm/T ++*; and 4, *++ sm/T Pl +*												
T1-6c	3	211	205	4	11	5	3	0	0	439	3.4	1.8
T2-6a	4	121	43	7	11	3	3	0	0	188	9.6	3.2
T2-6c	3	117	134	9	4	10	6	0	1	281	5.0	6.0
T2-6d	3	48	36	2	8	2	2	0	3	101	12.9	6.9
T2-6e	3	84	86	3	8	5	2	0	1	189	6.3	4.2
T3-6a	3	93	108	2	4	6	6	0	0	219	2.7	5.5
T4-6b	3	62	—	—	2	—	1	0	—	65	3.1	1.5
	3	124	—	11	—	15	—	0	—	150	7.3	10.0
T4-6c	3	156	65	124	18	19	3	4	1	390	37.7	6.9
T6-8a	3	102	79	1	2	2	1	0	2	189	2.6	2.6
T6-9b	3	190	263	14	18	8	9	1	4	507	7.3	4.3
T6-10b	4	60	61	8	4	4	1	0	0	138	8.7	3.6
Genotypic group 5, *+ sm + /Pl + T*												
T2-6b	5	350	320	27	28	14	11	3	0	753	7.7	3.7
T6-10a	5	138	146	13	13	37	43	2	1	393	7.4	21.1
Genotypic group 6, *++ py/T Pl +*												
T3-6a	6	24	47	1	1	6	2	1	0	82	3.7	11.0
Genotypic group 7, *++ py/sm T +*												
T6-10a	7	—	82	14	—	3	—	—	1	100	15.0	4.0

Results of three-point backcross tests are presented in table 2 for 13 translocations. Tests were made with F_1 plants which can be grouped into 7 genotypes. For example, genotypic groups 1 and 2 are alike in that they include translocations in which the order was *Y-T-Pl*, but they differ in linkage phase. The genotypic group is indicated in the second column of the table. The order of presentation of the data follows that of EMERSON *et al.* (1935) and the recombination values for both regions are in the last two columns.

In many instances, particularly in the preliminary stages of determining the

TABLE 3

Summary of two-point linkage tests

Translocation	Region					
	T-Y			*T-Pl*		
	Number	Recombinations	Percent	Number	Recombinations	Percent
T1-6c	405	4	1.0	404	22	5.4
T1-6g	—	—	—	154	36	23.4
T1-6h	258	9	3.5	—	—	—
T2-6b	—	—	—	401	47	11.7
T2-6d	—	—	—	208	3	1.4
T2-6e	170	8	4.7	156	6	3.8
T3-6a	219	13	5.9	581	16	2.8
T3-6b	231	36	15.6	219	57	26.0
T4-6b	1179	66	5.6	—	—	—
T4-6c	345	42	12.2	97	27	27.8
T5-6a	—	—	—	113	0	0.0
T5-6b	167	32	19.2	160	55	34.4
T5-6c	—	—	—	207	20	9.7
T5-6f	38	4	10.5	—	—	—
T6-8a	371	40	10.8	—	—	—
T6-9c	542	2	0.4	286	13	4.5
T6-9e	269	0	0.0	—	—	—
T6-10b	—	—	—	236	18	7.6

chromosomes involved in a translocation, two-point tests were made either with *Y* or *Pl*. These additional data are presented in table 3.

SUMMARY OF INDIVIDUAL TRANSLOCATIONS

The cytological positions given in table 1, the three-point data in table 2, the additional two-point data presented in table 3, and previously published data, can be used to arrange the translocations in the approximate order of the position of their breaks from left to right on chromosome 6. Such an arrangement is suggested in table 4. In a few instances, linkage data from homozygous interchange stocks were obtained to aid in establishing the order more definitely. The following brief summary for each translocation indicates the extent and limitations of the available data.

T1-6a. The break is in the distal half of the long arm of 6. Three-point data of BRINK and COOPER (1932) place it 8.2 units to the right of *Pl*.

T1-6b. BURNHAM (1932) has determined the break in 6 to be in the satellite region. His recombination values of *T*-13.8-*Y* and *T*-44.9 *Pl* (from EMERSON *et al.* 1935) agree in placing it well to the left of *Y*.

T1-6c. In spite of some inconsistency in the *T-Pl* recombinations from two 3-point tests in table 2, the break definitely appears to be to the left of *Pl* and near *Y*. ANDERSON (1941) placed the break on 1 to the right of *P*. The positions at 1S.2 and 6L.4 would indicate the break to be proximal both to *P* and to *Pl*. This is confirmed in the homozygous translocation where *P* showed 46.4 percent recombination with *Pl* which for 293 plants is not significantly different from independence.

TABLE 4

The approximate order from left to right of chromosome 6 translocations

Translocation	Gene order and recombination							Position on chromosome 6
T3-6b	*T*	15.6 (231)	*Y*					S.77[s]
*T1-6b**	*T*	13.8 (130)	*Y*					S[s]
T4-6c	*T*	8.4 (479)	*Y*	23.0 (152)	*Pl*	6.9 (390)	*sm*	S.83[s]
T6-9a†	*T*	12.9 (402)	*Y*	22.4 (402)	*Pl*			S.79[o]
T5-6f	*T*	10.5 (38)	*Y*					S.70[o]
T5-6c	*T*			9.7 (207)	*Pl*			S.11
T2-6a	*T*			9.6 (188)	*Pl*			S.09
T4-6b	*T*	5.6 (1098)	*Y*	9.3 (290)	*Pl*	10.3 (290)	*sm*	L.14
T1-6h	*T*	3.5 (258)	*Y*					L.16
T6-10b	*T*			8.2 (417)	*Pl*	3.6 (138)	*sm*	L.18
T6-9b	*Y*	1.4 (515)	*T*	5.5 (2218)	*Pl*	4.3 (507)	*sm*	L.13
T6-9c	*Y*	0.4 (542)	*T*	4.5 (286)	*Pl*	4.2 (189)	*sm*	L.17
T6-9e	*Y*	0.0 (269)	*T*					L.17
T2-6c			*T*	5.0 (281)	*Pl*	6.0 (281)	*sm*	L.20
T2-6e	*Y*	4.7 (170)	*T*	5.2 (345)	*Pl*	4.2 (189)	*sm*	L.22
T1-6c	*Y*	1.0 (605)	*T*	5.7 (1043)	*Pl*	1.8 (439)	*sm*	L.39
T4-6a‡	*Y*	1.3 (389)	*T*	5.3 (1025)	*Pl*	5.5 (325)	*sm*	L.44
T3-6a	*Y*	6.7 (345)	*T*	3.1 (1007)	*Pl*	5.5 (219)	*sm*	L.26
T6-8a	*Y*	11.3 (789)	*T*	4.9 (427)	*Pl*	2.6 (189)	*sm*	L.41
T2-6d			*T*	5.2 (309)	*Pl*	6.9 (101)	*sm*	L.45
T5-6a			*T*	0.0 (113)	*Pl*			L.47
T1-6a§	*Y*	39.8 (98)	*Pl*	8.2 (98)	*T*			L.59
T2-6b			*Pl*	7.7 (753)	*sm*	3.7 (753)	*T*	L.49
T1-6g			*Pl*	23.4 (154)			*T*	L.84
T6-10a	*Pl*	9.5 (493)	*sm*	17.0 (100)	*py*	3.0 (134)	*T*	L.68

* Data of C. R. BURNHAM from EMERSON *et al.* (1935).
† Data of ANDERSON (1934).
‡ Data of ANDERSON (1952).
§ Data of BRINK and COOPER (1932).
[s] Satellite. [o] Organizer.

T1-6g. The position at 6L.84 and 23.4 percent recombination for *T-Pl* suggest the break to be well beyond *Pl.*

T1-6h. The data in table 3 indicate only that the translocation is in the general region of *Y.*

T2-6a. Cytological placement is 6S.09. The order *T*-9.6-*Pl-sm* is in agreement.

T2-6b. The break at 6L.49 is definitely to the right of *sm.*

T2-6c. The interchange is at 6L.20 and 5 units to the left of *Pl.*

T2-6d. The three-point test in table 3 gave the order *T-Pl-sm.* Cytological positions are in the long arms both of 2 and 6. Extensive tests with the homozygous translocations showed independence of *Pl* and v_4 on the long arm of two (49.3 percent recombination for 1265 plants), but linkage of *Pl* with *B* on the short arm of 2. (36.4 percent, 1656 plants). These results confirm the placements on the long arms of both chromosomes with breaks proximal both to *Pl* and v_4.

T2-6e. The conclusions are similar to *T2-6d.* Data for the heterozygous translocation indicate the order *T-Pl-sm.* Cytological positions are on the long arms of both

chromosomes. In the homozygous translocation there was 50.8 percent (222/437) recombination for *Pl-v*$_4$ and 12.2 percent (20/164) for *Pl-B*.

T3-6a. Data from 3 different genotypes in table 2 agree in placing the interchange to the left of *Pl*. In genotype 2, the *Y* + +/+ *T Pl* plant was used as the pollen parent and it is possible that some pale yellow seeds were classified as white, thus inflating one crossover class in region 1. The interchange, therefore, while it appears to be to the left of *Y* can not be established with certainty from these data.

T3-6b. The interchange is in the satellite region and the two-point data in table 3 agree in placing it well to the left of *Y*.

T4-6a. ANDERSON (1952) has completely characterized this translocation. The break is at or very near *Y*, possibly to the left.

T4-6b. Partial 3-point data are available on two cultures. In one, difficulty was experienced in classifying for *sm* and only data from 65 *sm* plants are considered reliable. In a second culture, a marked deficiency of semisterile plants was noted and the data from 150 normal plants are presented. The larger culture more definitely places the interchange to the left of *Pl* but the recombination values are probably inflated because of the excess of non-semisterile plants. The 2-point data with *Y* in table 3 also were found to be somewhat variable with values ranging from less than 2 to more than 7 percent. The interchange is probably to the left of *Pl* but its position relative to *Y* is uncertain.

T4-6c. Both cytological and genetic data place the break well to left of *Y*.

T5-6a. With the interchange at 6L.47, no crossover in the *T-Pl* region was observed among 113 plants.

T5-6c. Cytological placement is on the short arm but near the centromere.

T5-6f. Although only 38 plants were tested, 10.5 per cent recombination for the *T-Y* region is consistent with the cytological placement on the short arm.

T6-8a. The interchange appears to be to the right of *Y* but its position with respect to *Pl* remains uncertain. In the homozygous translocation, *Y* shows 16.1 percent (20/124) recombination with *j* on the long arm of 8. Since ANDERSON (1939) gives the order *T*-7.8-*ms*$_8$-*j* for chromosome 8 this translocation is distal to *Y* and proximal to *j*.

T6-9a. The break on chromosome 6 is in the nucleolus organizer region. ANDERSON (1934) showed the order to be *T-Y-Pl*. In 3-point backcross tests with the F_1 used as a female his values were *T*-4.9-*Y*-16.2 *Pl* for 142 plants, while for the F_1 used as a male the values were *T*-17.3-*Y*-25.8 *Pl* for 260 plants. The higher values appear more in line with the break in the organizer region.

T6-9b. The position appears definitely to be between *Y* and *Pl*. In homozygous tests *Pl* and *sm* remained linked. *Pl* and *wx* are independent in the homozygote showing that the interchange at 6L.13, 9S.42 is proximal both to *Pl* on 6 and *wx* on 9.

T6-9c. The data in table 3 indicate only that the break at 6L.17 is near *Y*.

T6-9e. With the break at 6L.22, no recombinants with *Y* were found in 269 plants.

T6-10a. At 6L.68, the break is definitely to the right of *sm*. In the homozygous translocation *Pl* and *sm* remain linked (7 recombinants in 78 plants). Partial data in table 2 in which data from the non-pigmy plants was considered reliable indicates that the break is probably beyond *py*.

T6-10b. The break at 6L.18 is proximal to *Pl*.

SUPPRESSION OF RECOMBINATION IN CHROMOSOME 6

In table 4 it will be observed that all translocations in which the interchange is known to be between *Y* and *Pl* show less than 10 percent recombination of *Y* with *Pl*. One possible exception is *T6-8a* but here the point of interchange with respect to *Pl* is uncertain. This reduction in recombination makes translocations involving chromosome 6 particularly valuable since *Y* is a non-defective readily classified endosperm character.

SUMMARY

A recent revision of the interchange positions of 46 translocations involving chromosome 6 is presented in table 1.

Three-point linkage data are presented for 13 translocations and additional two-point data are included for certain of these and for 8 additional translocations. These 21 together with 4 previously described translocations have been arranged in their approximate order from left to right on chromosome 6.

All translocations in the proximal half of the long arm show low recombination values with *Y*, and those between *Y* and *Pl* reduce the *Y-Pl* recombination from the standard map distance of 31 units to less than 10 percent.

ACKNOWLEDGMENTS

The second writer gratefully acknowledges the Gosney fellowship of the California Institute of Technology and the sabbatical leave from Purdue University which made possible his assistance in the analysis of the data.

LITERATURE CITED

ANDERSON, E. G., 1934 A chromosomal interchange in maize involving the attachment to the nucleolus. Am. Naturalist **68:** 345–350.

1935 Chromosomal interchanges in maize. Genetics **20:** 70–83.

1938 Translocations in maize involving chromosome 9. Genetics **23:** 307–313.

1939 Translocations in maize involving chromosome 8. Genetics **24:** 385–390.

1941 Translocations in maize involving the short arm of chromosome 1. Genetics **26:** 452–459.

1952 A chromosomal technique used in biochemical studies on the developing endosperm of maize. Agron. J. **44:** 560–561.

ANDERSON, E. G., and R. A. BRINK, 1940 Translocations in maize involving chromosome 3. Genetics **25:** 299–309.

ANDERSON, E. G., and H. H. KRAMER, 1954 Translocations in maize involving chromosome 10. Genetics **39:** 506–512.

ANDERSON, E. G., H. H. KRAMER, and A. E. LONGLEY, 1955 Translocations in maize involving chromosome 4. Genetics 40: 500–510.

ANDERSON, E. G., and L. F. RANDOLPH, 1945 Location of the centromeres on the linkage maps of maize. Genetics **30:** 518–526.

BRINK, R. A., and D. C. COOPER, 1932 A strain of maize homozygous for segmental interchanges involving both ends of the P-Br chromosome. Proc. Nat. Acad. Sci. U. S. **18:** 441–447.

BURNHAM, C. R., 1932 An interchange in maize giving low sterility and chain formation. Proc. Nat. Acad. Sci. U. S. **18:** 434–440.

1949 Chromosome segregation in maize translocations in relation to crossing over in interstitial segments. Proc. Nat. Acad. Sci. U. S. **35:** 349–556.

1950 Chromosome segregation in translocations involving chromosome 6 in maize. Genetics **35:** 446–481.

BURNHAM, C. R., and J. L. CARTLEDGE, 1939 Linkage relations between smut resistance and semi-sterility in maize. J. Am. Soc. Agron. **31:** 924–933.

EMERSON, R. A., G. W. BEADLE, and A. C. FRASER, 1935 A summary of linkage studies in maize. Cornell U. Agr. Exp. Sta. Mem. **180:** 1–83.

IBRAHIM, M. A., 1954 Association tests between chromosomal interchanges in maize and resistance to the European corn borer. Agron. J. **46:** 293–298.

MCCLINTOCK, BARBARA, 1931 Cytological observations of deficiencies involving known genes, translocations and an inversion in *Zea mays*. Mo. Agr. Exp. Sta. Res. Bul. **163:** 1–30.

RHOADES, M. M., 1950 Meiosis in maize. J. Heredity **41:** 58–67.

ROBERTS, L. M., 1942 The effects of translocation on growth in *Zea mays*. Genetics **27:** 584–603.

SABOE, L. C., and H. K. HAYES, 1941 Genetic studies of reaction to smut and of firing by means of chromosomal translocations. J. Am. Soc. Agron. **33:** 463–470.

TEAS, H. J., J. W. CAMERON, and ANNA C. NEWTON, 1952 Tryptophan, niacin, indoleacetic acid, and carbohydrates in developing sugary and starchy maize kernels. Agron. J. **44:** 434–438.