Transmission of Duplication-Deficiencies from Cotton Translocations Is Unrelated to Map Lengths of the Unbalanced Segments

Margaret Y. Menzel and Brian J. Dougherty

Department of Biological Science, Florida State University, Tallahassee, Florida 32306-3050

Manuscript received July 1, 1986
Revised copy accepted February 20, 1987

ABSTRACT

Adjacent-1 duplication-deficiencies (dp-dfs) are readily recovered from most heterozygous translocations in *Gossypium hirsutum* L., but frequencies of specific cytotypes differ widely in progenies from heterozygote (♀) × standard crosses. Surprisingly, these frequencies seem to be unrelated to the primary (postmeiotic) frequencies predicted by metaphase I configurations or to the proportion of the chromosome arm that is duplicate or deficient. Deficiencies and duplications from different translocations involving the same arm, as well as the two complementary dp-dfs from the same translocation, seldom exhibit similar frequencies. We conclude that the frequency of each of 101 different adjacent-1 cytotypes is largely idiosyncratic and may depend in part on interactions between the specific chromosome regions that are respectively trisegmental and monosegmental. Few, if any, of these interactions can be between homoeologues of the A_h and D_h genomes. Adjacent-2 dp-dfs are seldom recovered, even if they involve chromosomes that are readily tolerated in monosomic condition. Comparison of monosomes and telosomes with deficiencies suggests that some chromosomes and chromosome regions may be more dosage-sensitive than others, but their identification is not strongly supported by these data.

RECIPROCAL translocations are the primary reference set of chromosome markers for upland cotton (*Gossypium hirsutum* L.) (BROWN 1980). A map of chromosome locations of 116 breakpoints in 58 translocation lines, based on interstitial and distal chiasma frequencies in translocation heterozygotes, is available (MENZEL, RICHMOND and DOUGHERTY 1985). Breakpoint map distances have been shown to correspond rather closely to recombination map distances for chromosome *15* (MENZEL and RICHMOND 1986) and *16* (M. Y. MENZEL and K. L. RICHMOND, unpublished data), as would be expected from the standard cytogenetic assumption that one chiasma equals 50 cM (centimorgans). (Tests of several other chromosomes are in progress.)

In cotton, duplication-deficiencies (dp-dfs) arising from adjacent-1 disjunction of the heterozygous translocation quadrivalent are often ovule-viable and occasionally pollen-viable as well (MENZEL and BROWN 1952, 1954, 1978; MENZEL and RICHMOND 1986). From 56 translocation lines investigated, 101 adjacent-1 dp-df cytotypes were identified and characterized cytologically and morphologically (MENZEL *et al.* 1986). Deficiencies were found to exert a much greater effect on the phenotype than did duplications. The dp-dfs are useful for chromosome analysis and manipulation in cotton [*e.g.*, MENZEL and RICHMOND (1986)].

The frequencies with which specific dp-dfs are recovered differ widely. In this paper, we examine factors that might influence the frequencies and show that, contrary to intuition [and see RHOADES and DEMPSEY (1953)], frequency does not appear to be related either to the meiotic frequency of unbalanced products or to the relative map lengths of the duplicate or deficient segments.

MATERIALS AND METHODS

Gossypium hirsutum is an allotetraploid ($2n = 52$; genome formula $2(AD)_1$). The individual 13-chromosome genomes are referred to as A_h and D_h and their chromosomes as *H1-H13* and *H14-H26*, respectively.

The experimental methods and the data discussed here have been described previously (MENZEL, RICHMOND and DOUGHERTY 1985; MENZEL *et al.* 1986). Briefly, plants homozygous for each of 56 different translocations were crossed to the standard line TM-1, and the resulting heterozygotes were backcrossed as ovule parents to TM-1 to generate for each translocation line one or more 50-plant progenies in which dp-df plants (as well as plants with balanced chromosome constitutions) were expected. About 75% of the specific dp-df cytotypes could be recognized by distinctive morphological traits. All plants included in the present study were verified cytologically. Cytological and morphological data for each dp-df plant were coded with an Apple IIe computer to facilitate data collation and analysis.

In the BC_1 progenies, 3339 plants were analyzed, and 867 had unbalanced cytotypes, of which 725 were attributed to adjacent-1 and 11 to adjacent-2 disjunction. Of the adjacent-1 dp-dfs, 689 could be assigned to one of 101 specific cytotypes by a combination of cytological and morphological criteria, and the frequency of each type could be determined. In the present paper, the frequencies with which the two complementary adjacent-1 dp-dfs were recovered are

compared with various other parameters in an attempt to identify factors that might account for the widely disparate frequencies of various cytotypes. Statistical analyses were performed by Minitab on the Florida State University CYBER 730 computer. In analyzing the data, procedures designed for the comparison of frequency data were used wherever possible. All χ^2 values reported have been corrected for continuity.

RESULTS AND DISCUSSION

Do the frequencies of meiotic orientations of the translocated chromosomes account for the frequencies of duplication-deficiency plants? The primary (postmeiotic) frequencies of unbalanced meiotic products are of course predicted by the metaphase I orientations of the four chromosomes involved in the heterozygous translocations. We calculated these frequencies (Table 1) from pollen mother cells (PMCs) of heterozygotes in the BC_1 progenies (MENZEL *et al.* 1986). In general, they are similar to those reported by BROWN *et al.* (1981). Meiotic orientations have not been determined for embryo sac mother cells in cotton, but here are assumed to be similar to those of PMCs.

In a total of 10,793 PMCs from translocation heterozygotes, the overall frequency of numerically balanced dp-df meiotic products in the 56 lines was calculated to be 55.99%, whereas among 3339 plants analyzed, the overall frequency of dp-dfs was 21.41%, or 38% of the primary frequency. It is evident that there is considerable selection against genetically unbalanced spores, gametes, and/or zygotes.

However, the severity of selection differs widely among lines. The heterogeneity of recovery rates was highly significant ($P < 0.005$) for the overall sample (all arms with breakpoints), for A_h arms, for D_h arms, for chromosomes represented by monosomes, for chromosomes not represented by monosomes, and for chromosomes represented by telosomes for one arm but not by monosomes (χ^2 tests) (SNEDECOR and COCHRAN 1967).

The predicted rates of recovery of adjacent-1 dp-dfs were also heterogeneous for the overall sample and the subsets listed above (except the last), but the difference between observed and predicted recovery rates is significant for 23 of 31 arms tested, for the overall sample and all subsets listed above (including the last).

When primary frequencies of numerically balanced products were compared with the frequencies of dp-df plants in the BC_1 progenies, the rate of recovery ranged from 0 to 86% of the primary rate (Table 1). The frequencies with which dp-df meiotic products were generated were essentially uncorrelated with the frequencies of the corresponding unbalanced cytotypes ($r = -0.046$).

Adjacent-1 *vs.* adjacent-2 duplication-deficiencies: Plants with identified adjacent-1 cytotypes outnumbered those with adjacent-2 cytotypes 65:1. Even if all of the 36 dp-df plants that could not be assigned to specific cytotypes were actually from adjacent-2 disjunction, the ratio would still be 15:1 in favor of adjacent-1.

Orientation of multivalents depends on a number of (poorly defined) mechanical factors, and not on homology of centromeres [*e.g.*, see LEWIS and JOHN (1966); ENDRIZZI (1974); ENDRIZZI, RAY and GATHMAN (1983) and RICKARDS (1983)]. The actual frequencies of alternate and adjacent orientations will therefore be specific to each individual translocation. To determine whether an excess of adjacent-1 orientations accounts for the rarity of adjacent-2 dp-dfs, we estimated the frequencies (Table 1) of adjacent-1 and adjacent-2 orientations by the criteria shown in Table 2.

In 19 lines, the modal configuration formed by the translocated chromosomes in heterozygotes is a quadrivalent (IV) with one or two interstitial chiasmata. Such configurations virtually never exhibit adjacent-2 orientations, and the predicted frequencies of adjacent-2 dp-df products is correspondingly low (0.0–9.56).

A majority (37) of the lines form ring IVs as the modal configurations in heterozygotes. For many of these lines, two different adjacent orientations can be discerned, but we do not know which is adjacent-1 and which adjacent-2. The calculated adjacent-2 frequencies (17.09–34.64%) may be either under- or overestimates.

In one example, *T15R;16R* 2767, among 82 PMCs with adjacent orientations suitable for this determination, 46 had "type A" and 36 had "type B" configurations. This ratio is not significantly different from the calculated primary ratio of 44.24 adjacent-1:37.76 adjacent-2 (Table 2), regardless of which configuration is type A and which is type B ($\chi^2 = 2.94$, $0.10 > P > 0.05$ even if type B is adjacent-1). The four types of dp-df plants from this translocation can be distinguished unequivocally by a combination of cytological and phenotypic traits (M. Y. MENZEL and K. L. RICHMOND, unpublished data). Among a total of 194 BC_1 plants from two experiments, 51 adjacent-1 and 4 adjacent-2 dp-df plants were identified, whereas 70 and 60, respectively, would have been predicted on the assumption that adjacent-1 orientations are the more common (type A). One adjacent-2 cytotype, *dp16L;df15L*, was absent in these progenies.

It appears, therefore, that selection is much more severe against adjacent-2 than against adjacent-1 gametes. It might be supposed that this difference ensues from the fact that adjacent-1 products are unbalanced only for the chromosome segments distal to the breakpoints, whereas the adjacent-2 products are unbalanced for the unbroken arms, the centromeres, and the segments proximal to the breakpoints. However

TABLE 1

Frequencies of orientations *vs.* frequency of dp-dfs

Translocation and line		Total plants	Total hets	Total het PMCs	Observed frequency orientations (%)			Observed frequency dp-dfs in progeny	Dp-df survival rate (frequency dp-df/frequency adj.) (%)	Calculated frequency[a]	
					Alt.	Adj.	Other			Adj.-1	Adj.-2
1L;2L	*DP30*	67	30	154	38.31	58.77	2.92	13.43	22.85	31.33	27.44
1L;3L	*2935*	57	27	188	46.01	53.46	0.53	14.04	26.26	35.11	18.35
1L;7L	*5-4C*	48	26	160	36.88	62.50	0.63	8.33	13.33	33.13	29.38
1L;8L	*2775b*	94	42	237	43.46	55.49	1.05	10.64	19.17	29.43	26.05
1L;14L	*2780*	80	31	215	44.42	55.58	0.00	38.75	69.72	41.40	14.19
1L;20R	*4669*	57	23	146	39.04	60.96	0.00	31.58	51.80	31.16	29.79
1R;16R	*2770*	43	29	348	50.43	49.28	0.00	0.00	0.00	48.20	1.08
1R;16R	*4672*	40	19	211	48.34	50.24	0.00	2.50	4.98	48.58	1.66
2L;3L	*1059*	47	16	102	37.25	62.75	0.00	31.91	50.85	32.84	29.90
2L;6R	*7-2B*	46	19	124	47.58	51.61	0.81	23.91	46.33	27.62	23.99
2L;9R	*8B-3*	43	18	140	26.79	72.86	0.36	23.26	31.92	36.61	36.25
2R;3L	*IV*$_1$	50	24	128	45.70	53.52	0.78	16.00	29.90	27.73	25.78
2R;8R	*1039*	30	13	75	35.33	62.00	2.67	13.33	21.50	31.33	30.67
2R;8R	*1058b*	40	19	129	50.78	48.06	1.16	15.00	31.21	25.00	23.06
2R;14R	*2B-1*	68	11	68	50.00	48.53	0.00	39.71	81.83	48.53	0.00
3L;19L	*E20-7*	69	22	197	49.37	50.38	0.25	34.78	69.04	49.75	0.63
3R;5R	*8-5Gb*	40	19	236	50.85	49.15	0.00	15.00	30.52	42.37	6.78
3R;9R	*8-30-5*	46	13	72	45.83	54.17	0.00	21.74	40.13	44.44	9.72
4L;5R	*IV*$_2$	58	25	245	47.45	51.73	0.82	25.86	49.99	29.59	22.14
4L;19R	*10-5Ka*	89	36	248	43.85	54.74	1.41	30.34	55.43	36.09	18.65
4R;15L	*1040*	126	46	258	43.02	56.40	0.58	26.98	47.84	31.30	25.10
5L;9L	*C14-3*	33	10	57	29.82	70.18	0.00	21.21	30.22	37.28	32.89
5R;12R	*SL18*	46	16	168	40.77	58.63	0.60	34.78	59.32	34.82	23.81
5R;23R	*2775a*	58	30	359	56.41	43.59	0.00	12.07	27.69	36.56	7.03
6L;7L	*1048*	54	18	120	35.42	63.75	0.83	37.04	58.10	34.38	29.38
6L;14R	*AZ-7*[b]	92	48	280	39.64	59.29	1.07	14.13	23.83	31.96	27.32
6L;10R	*Z9-9*	77	38	250	30.20	68.60	1.20	19.48	28.40	35.80	32.80
7L;12R	*1043*	47	14	112	29.91	69.20	0.89	29.79	43.05	40.85	28.35
7L;18R	*4659*	44	16	188	32.98	66.49	0.53	20.45	30.76	36.44	30.05
7R;11R	*1052*	73	20	113	51.33	48.67	0.00	39.73	81.63	45.13	3.54
7R;21R	*2790*	52	27	309	50.32	49.03	0.00	23.08	47.07	48.87	0.16
8R;12L	*2778*	94	41	264	49.34	50.47	0.19	27.66	54.80	49.34	1.14
8R;19R	*5-5B*	55	31	369	34.69	65.04	0.27	1.82	2.80	37.47	27.57
9L;17R	*1036*	20	9	97	44.33	52.06	3.61	45.00	86.44	30.41	21.65
9L;17R	*6340*	43	23	167	36.98	61.53	1.50	32.56	52.92	33.38	28.14
9L;25?	*2870*	36	17	105	42.86	56.19	0.95	27.78	49.44	29.76	26.43
9R;20L	*2772*	45	34	264	50.38	49.62	0.00	15.56	31.36	47.16	2.46
10L;21L	*4675*	70	35	239	48.12	51.05	0.84	15.71	30.77	46.76	4.29
10R;11R	*2785*	63	38	180	41.94	56.39	1.67	7.94	14.08	36.39	20.00
10R;19R	*1626*	50	22	140	22.50	73.93	3.57	14.00	18.94	39.29	34.64
11L;15L	*1058a*	96	48	288	42.88	57.12	0.00	10.42	18.24	37.76	19.36
11R;12L	*6-5M*	68	31	183	51.91	47.54	0.55	32.35	68.05	39.48	8.06
11R;13L	*10-5Kb*	39	15	98	49.49	50.51	0.00	23.08	45.69	40.05	10.46
11R;17R	*1316*	80	12	79	43.67	56.33	0.00	32.50	57.70	39.24	17.09
12R;19R	*9-5H*	57	26	229	38.97	57.97	3.06	35.09	60.53	31.33	26.64
13R;19R	*2925*	95	24	385	48.51	48.25	0.13	26.32	54.55	48.05	0.19
14L;23R	*2777*	58	23	280	49.46	50.54	0.00	24.14	47.76	47.50	3.04
14L;24R	*2781*[b]	72	38	249	24.50	73.29	2.21	9.72	13.26	39.26	34.04
15L;16R	*8-5Ga*[b]	79	38	259	42.66	55.79	1.54	10.13	18.16	46.24	9.56
15R;16R	*2767*[b]	50	20	114	33.33	66.67	0.00	36.00	54.00	35.96	30.70
15R;20R	*SL15*	96	35	238	37.92	61.45	0.63	29.17	47.47	40.34	21.11
19L;21R	*E22-13*	49	33	335	50.22	49.63	0.15	8.16	16.44	49.03	0.60
19R;24R	*2786*	83	51	269	36.43	63.20	0.37	3.61	5.71	33.92	29.28
20L;22R	*DP4*	51	22	113	45.13	54.87	0.00	23.53	42.88	33.41	21.46
20R;21L	*7-3F*	47	23	155	47.58	51.13	0.65	14.89	29.12	43.39	7.74
20R;25R	*2791*	29	10	57	32.46	67.54	0.00	13.79	20.42	38.16	29.39

Alt. = alternate; Adj. = adjacent.

[a] Frequencies assigned on the assumptions shown in Table 2.

[b] MENZEL *et al.* (1986) assigned line *AZ-7* to *T6L;14L*, line *2781* to *I14R;24R*, line *8-5Ga* to *T15R;16L* and line *2767* to *T15L;16L*. Later data from linkage tests and telosome tests showed that four of these arm assignments were incorrect (M. Y. MENZEL and K. L. RICHMOND, unpublished data). The correct assignments are shown here and in Tables 3, 4 and 6.

TABLE 2

Criteria used to estimate the frequencies of balanced, adjacent-1, and adjacent-2 meiotic products in cotton translocation heterozygotes

Configurations	Percent		
	Balanced	Adjacent-1	Adjacent-2
Alternate ring and chain IVs	100		
Adjacent ring and chain IVs		50	50
IVs with one or two interstitial chiasmata	50	50	
All other configurations	50	25	25

(see below), the frequencies of dp-df plants are not correlated with the lengths of the chromosome segments that are duplicate or deficient. Nor is dosage of centromere regions *per se* likely to be the cause, inasmuch as monosomes are known for 15 of the chromosomes, and trisomes are readily tolerated with very little effect on the phenotype. The heavy selection against adjacent-2 products remains unexplained.

Frequencies of complementary adjacent-1 duplication-deficiencies from the same translocation: The primary frequencies of complementary dp-dfs must be equal, since a meiotic division that gives rise to one must give rise to an equal number of the other. Adjacent-1 orientation of a ring quadrivalent will give rise to two spores of each type; quadrivalents with one interstitial chiasma will yield tetratype sporads containing two balanced and two complementary unbalanced spores; quadrivalents with chiasmata in both interstitial regions will exhibit second-division segregations that, on the average, will produce equal numbers of the two dp-df types, and so forth.

However, the frequency of one of the two types does not predict the frequency of the other in the BC_1 progenies (Table 3). The transmission rate of one cytotype is not correlated with the transmission rate of the complementary type ($r = 0.088$).

We conclude that differences in the primary frequencies with which the various dp-dfs are generated are obscured by differential viability at some stage or stages before the seedlings are established. A cursory comparison of germination and seedling survival rates among lines suggested that most of the selection occurs before seed maturation. CONTOLINI and MENZEL (1987) investigated the developmental stages at which dp-df products were lost in heterozygotes of *T10;11 2785* and concluded that loss occurs in this line prior to 5 days after anthesis and may occur primarily at fertilization (*i.e.*, after pollen tube growth down the style but before the first embryonic division).

Is the frequency of deficiencies recovered related to the proportion of the chromosome that is monosegmental? Duplications of chromosomes and chromosome segments in cotton usually have little effect on viability or on morphological characteristics. However, monosomes, telosomes, and segmental deficiencies usually produce recognizable phenotypic effects and often affect vigor and fertility adversely (ENDRIZZI, TURCOTTE and KOHEL 1985; MENZEL *et al.* 1986). We expected that the effect of dp-dfs on viability would be proportional to the length of the chromosome segment missing in the gametophyte or monosegmental in the sporophyte.

To test this hypothesis, we standardized the length of each duplicate or deficient segment to the percentage of the chromosome arm map length (MENZEL, RICHMOND and DOUGHERTY 1985) that was distal to each breakpoint (Table 3). (The relationships of map lengths to actual physical lengths of chromosome segments is unknown.) Inspection of the frequencies of deficiencies and of duplications from different translocations involving the same chromosome arm suggested that there was no systematic relationship between distance of the breakpoint from the centromere and frequency of viable monosegmental or trisegmental plants. We then plotted the frequency of 101 deficiency cytotypes against the percentage of arm missing and found no obvious relationship between the two.

To determine whether these conclusions were statistically valid, we used multiple linear regression and Spearman rank correlation analyses. The Spearman rank correlation is a nonparametric statistical procedure. Nonparametric procedures do not require that the data be drawn from a normal distribution. The Spearman correlation was used to investigate whether the order of breakpoints, in relation to the centromere, could be used to predict the relative order of recovery of deficiencies.

In the multiple regression analysis, variables for breakpoint location, adjacent orientation, and percent of chromosome arm duplicate or deficient were used. In addition, three dummy variables were used to indicate whether the chromosomes involved in the translocation came both from the A_h genome, both from the D_h, or one from each genome. The data were regressed untransformed, fully transformed to $\log_{10}$, and fully transformed to arcsin square root (the recommended transformation for frequency data). The highest R^2 obtained was 0.023 for the fully $\log_{10}$ transformed data. This value fell to less than 0.00 when adjusted for degrees of freedom.

The Spearman rank correlation coefficients were also very low. The frequency of adjacent-1 orientations had the highest correlation with the frequency of dp-dfs recovered ($\rho = -0.030$).

A similar treatment of duplications likewise revealed negligible correlation. Contrary to expectation, the proportion of the map length that is mono- or

TABLE 3

Percent of chromosome (Chr.) arm (map length) deficient or duplicate *vs.* frequency of recovery of monosegmental and trisegmental plants in BC_1 progeny for 54 cotton translocations (adjacent-1 only)

Chr. arm	Arm length (cM)	Translocation and line	Breakpoint location ± SD[a]	Uncertainty[b]	Percent arm duplicate or deficient	Percent of progeny: Monosegmental	Percent of progeny: Trisegmental	No. plants analyzed
*1*L	56.40	*1L;20R 4669*	0.4 ± 0.5	0.4	99.28	17.54	12.28	57
		1L;2L DP30	2.5 ± 1.5	0.7	95.56	4.48	5.97	67
		1L;7L 5-4C	2.5 ± 1.2	1.3	95.56	4.17	4.17	48
		1L;8L 2775b	2.9 ± 1.1	1.0	94.86	7.45	3.19	94
		1L;3L 2935	9.0 ± 2.1	6.8	84.03	10.53	3.51	57
		1L;14L 2780	16.5 ± 2.5	1.3	70.74	31.25	7.50	80
*1*R	68.00	*1R;16R 4672*	30.0 ± 3.2	0.4	55.87	2.50	0.00	40
		1R;16R 2770	36.9 ± 2.6	0.8	45.73	0.00	0.00	43
2L	53.80	*2L;9R 8B-3*	0.2 ± 0.4	0.2	99.62	18.60	4.65	43
		2L;3L 1059	1.6 ± 1.1	0.8	97.03	25.53	4.26	47
		1L;2L DP30	2.5 ± 1.5	0.7	95.34	5.97	4.48	67
		2L;6R 7-2B	2.9 ± 1.5	2.1	94.61	17.39	6.52	46
2R	51.90	*2R;8R 1039*	0.0 ± 0.0	0.0	100	10.00	0.00	30
		2R;8R 1058b	1.3 ± 1.1	0.9	97.50	12.50	2.50	40
		2R;14R 2B-1	5.0 ± 2.7	0.4	90.37	19.12	20.59	68
3L	61.20	*3L;19L E20-7*	1.2 ± 0.8	0.2	98.03	17.39	17.39	69
		2L;3L 1059	1.6 ± 1.1	0.8	97.38	4.26	25.53	47
		1L;3L 2935	9.0 ± 2.1	6.8	85.28	3.51	10.53	57
3R	63.30	*3R;9R 8-30-5*	19.5 ± 4.7	15.3	69.18	8.70	13.04	46
		3R;5R 8-5Gb	27.0 ± 2.9	9.3	57.34	2.50	2.50	40
4L	46.30	*4L;19R 10-5Ka*	5.8 ± 1.5	1.1	87.46	22.47	1.12	89
4R	48.10	*4R;15L 1040*	3.9 ± 1.4	1.4	91.89	16.67	9.52	126
5L	45.00	*5L;9L C14-3*	3.0 ± 2.2	1.3	93.33	15.15	3.03	33
5R	60.20	*5R;12R SL18*	10.1 ± 2.4	0.2	83.21	15.22	10.87	46
		5R;23R 2775a	11.4 ± 1.7	0.8	81.06	5.17	6.90	58
		3R;5R 8-5Gb	27.0 ± 2.9	9.3	55.15	2.50	2.50	40
6L	51.40	*6L;7L 1048*	1.0 ± 1.1	1.0	98.05	18.52	18.52	54
		6L;14R AZ-7	1.5 ± 0.7	1.0	97.08	13.04	1.09	92
		6L;10R Z9-9	1.9 ± 0.9	1.4	96.30	15.58	3.90	77
6R	47.10	*2L;6R 7-2B*	2.9 ± 1.5	2.1	93.84	6.52	17.39	46
7L	58.90	*6L;7L 1048*	1.6 ± 1.4	1.0	97.28	18.52	18.52	54
		1L;7L 5-4C	2.5 ± 1.2	1.3	95.75	4.17	4.17	48
		7L;18R 4659	4.5 ± 1.4	1.0	92.36	11.36	9.09	44
		7L;12R 1043	4.8 ± 2.0	4.4	91.84	19.15	10.64	47
7R	78.00	*7R;11R 1052*	34.4 ± 4.5	8.9	55.90	12.33	26.03	73
		7R;21R 2790	45.5 ± 3.6	1.4	41.67	19.23	3.85	52
8L	47.70	*1L;8L 2775b*	2.7 ± 1.1	0.9	94.34	3.19	7.45	94
8R	52.50	*2R;8R 1039*	0.0 ± 0.0	0.0	100	0.00	10.00	30
		2R;8R 1058b	1.3 ± 1.1	0.9	97.52	2.50	12.50	40
		8R;12L 2778	3.6 ± 1.3	0.7	95.62	0.00	27.66	94
		8R;19R 5-5B	6.8 ± 1.4	0.6	87.05	1.82	0.00	55
9L	54.20	*9L;25? 2870*	0.5 ± 0.7	0.0	99.08	0.00	16.67	36
		5L;9L C14-3	3.0 ± 2.2	1.3	94.46	3.03	15.15	33
		9L;17R 6340	3.2 ± 1.4	1.4	94.09	16.28	16.28	43
		9L;17R 1036	4.9 ± 2.3	2.2	90.96	25.00	20.00	20
9R	75.00	*2L;9R 8B-3*	0.2 ± 0.4	0.2	99.72	4.65	18.60	43
		3R;9R 8-30-5	19.5 ± 4.7	15.3	74.00	13.04	8.70	46
		9R;20L 2772	36.1 ± 3.0	1.8	51.87	11.11	4.44	45
10L	73.20	*10L;21L 4675*	35.4 ± 3.1	0.7	51.64	10.00	5.71	70
10R	55.50	*6L;10R Z9-9*	1.9 ± 0.9	1.4	96.58	3.90	15.58	77
		10R;19R 1626	2.5 ± 1.3	1.5	95.50	6.00	6.00	50
		10R;11R 2785	10.5 ± 2.3	7.9	81.08	1.59	6.35	63
11L	52.30	*11L;15L 1058a*	5.7 ± 1.4	0.3	89.09	9.38	1.04	96
11R	78.00	*10R;11R 2785*	10.5 ± 2.3	7.9	86.53	6.35	1.59	63
		11R;17R 1316	11.9 ± 2.5	1.0	84.74	8.75	22.50	80
		11R;13L 10-5Kb	17.4 ± 3.8	13.3	77.68	12.82	10.26	39
		11R;12L 6-5M	22.2 ± 3.1	9.3	71.53	27.94	4.41	68
		7R;11R 1052	34.4 ± 4.5	8.9	55.90	26.03	12.33	73

TABLE 3—Continued

Chr. arm	Arm length (cM)	Translocation and line	Breakpoint location ± SD[a]	Uncertainty[b]	Percent arm duplicate or deficient	Percent of progeny: Monosegmental	Percent of progeny: Trisegmental	No. plants analyzed
*12*L	67.70	*11R;12L 6-5M*	21.6 ± 3.0	9.3	68.09	4.41	27.94	68
		8R;12L 2778	66.7 ± 3.3	0.7	11.81	27.66	0.00	94
*12*R	49.30	*12R;19R 9-5H*	4.0 ± 1.3	1.7	91.89	8.77	26.32	57
		7L;12R 1043	4.8 ± 2.0	4.4	90.25	10.64	19.15	47
		5R;12R SL18	5.0 ± 1.7	0.1	89.86	10.87	15.22	46
*13*L	54.90	*11R;13L 10-5Kb*	18.4 ± 3.9	13.3	66.48	10.26	12.82	39
*13*R	60.30	*13R;19R 2925*	45.7 ± 2.5	0.9	24.21	6.32	20.00	95
*14*L	84.40	*14L;24R 2781*	2.7 ± 1.0	2.1	94.08	5.56	2.78	72
		1L;14L 2780	23.7 ± 2.9	1.3	71.92	7.50	31.25	80
		14L;23R 2777	37.4 ± 2.9	7.6	55.68	5.17	18.97	58
*14*R	50.70	*6L;14R AZ-7*	4.5 ± 1.3	0.9	91.12	1.09	13.04	92
		2R;14R 2B-1	42.7 ± 6.1	0.4	15.77	20.59	19.12	68
*15*L	66.34	*4R;15L 1040*	6.0 ± 1.8	1.4	90.96	9.52	16.67	126
		11L;15L 1058a	16.0 ± 2.2	0.3	75.88	1.04	9.38	96
		15L;16R 8-5Ga	24.8 ± 2.7	12.7	62.62	2.53	7.59	79
*15*R	53.91	*15R;16R 2767*	4.0 ± 1.8	3.5	92.58	18.00	18.00	50
		15R;20R SL15	13.0 ± 2.2	6.9	75.89	23.96	5.21	96
*16*R	66.34	*15R;16R 2767*	4.0 ± 1.8	3.5	93.97	18.00	18.00	50
		15L;16R 8-5Ga	24.8 ± 2.7	12.7	62.59	7.59	2.53	79
		1R;16R 2770	42.6 ± 2.7	0.8	35.75	0.00	0.00	43
		1R;16R 4672	42.6 ± 3.4	0.4	35.75	0.00	2.50	40
*17*R	48.60	*9L;17R 6340*	3.8 ± 1.5	1.4	92.18	16.28	16.28	43
		11R;17R 1316	7.5 ± 2.0	1.0	84.56	22.50	8.75	80
		9L;17R 1036	8.7 ± 2.9	2.2	82.00	20.00	25.00	20
*18*R	46.10	*7L;18R 4659*	3.5 ± 1.2	1.0	92.40	9.09	11.36	44
*19*L	88.20	*19L;21R E22-13*	44.8 ± 2.7	3.4	49.20	6.12	2.04	49
		3L;19L E20-7	85.4 ± 1.2	0.2	3.16	17.39	17.39	69
*19*R	51.50	*12R;19R 9-5H*	2.7 ± 1.1	1.8	94.75	26.32	8.77	57
		19R;24R 2786	2.9 ± 1.1	1.9	94.37	0.00	3.61	83
		10R;19R 1626	5.4 ± 1.9	1.4	89.50	6.00	6.00	50
		8R;19R 5-5B	6.7 ± 1.3	0.6	86.99	0.00	1.82	55
		13R;19R 2925	7.0 ± 1.3	0.9	86.40	20.00	6.32	95
		4L;19R 10-5Ka	14.1 ± 2.3	1.1	72.62	1.12	22.47	89
*20*L	63.10	*20L;22R DP4*	7.3 ± 2.4	5.1	88.43	9.80	13.73	51
		9R;20L 2772	28.5 ± 2.8	1.8	54.82	4.44	11.11	45
*20*R	63.40	*1L;20R 4669*	5.8 ± 1.9	0.3	90.84	12.28	17.54	57
		20R;25R 2791	6.3 ± 3.4	2.4	90.06	3.45	10.34	29
		15R;20R SL15	13.0 ± 2.2	6.9	79.50	5.21	23.96	96
		20R;21L 7-3F	19.4 ± 3.3	15.4	69.40	10.64	4.26	47
*21*L	75.80	*20R;21L 7-3F*	19.4 ± 3.3	15.4	74.40	4.26	10.64	47
		10L;21L 4675	35.8 ± 3.1	0.7	52.76	5.71	10.00	70
*21*R	88.20	*7R;21R 2790*	18.2 ± 2.8	1.3	79.37	3.85	19.23	52
		19L;21R E22-13	45.0 ± 2.7	3.4	48.98	2.04	6.12	49
*22*R	51.80	*20L;22R DP4*	7.3 ± 2.4	5.1	85.90	13.73	9.80	51
*23*R	73.70	*5R;23R 2775a*	21.3 ± 2.2	0.9	71.09	6.90	5.17	58
		14L;23R 2777	37.4 ± 2.9	7.6	49.25	18.97	5.17	58
*24*R	46.10	*14L;24R 2781*	2.7 ± 1.0	2.1	94.14	2.78	5.56	72
		19R;24R 2786	2.9 ± 1.1	1.9	93.71	3.61	0.00	83
*25*R	47.20	*20R;25R 2791*	6.3 ± 3.4	2.4	86.65	10.34	3.45	29

[a] These calculations are based upon the plotted map position (MENZEL, RICHMOND and DOUGHERTY 1985). Breakpoint location is in centimorgans from centromere. Standard deviation is based on the binomial approximation SD = $\sqrt{pq/n}$, where p = proportion of cells with interstitial chiasmata, $q = 1 - p$, and n = total cells.

[b] The uncertainty represents one half the difference between minimum and maximum estimates of the location of the breakpoint. The uncertainty in the breakpoint location estimates is due to the difficulty of determining precisely which regions are chiasmate in a translocation quadrivalent (MENZEL, RICHMOND and DOUGHERTY 1985).

trisegmental does not appear to be a significant factor in recovery rate.

The precision with which the positions of the breakpoints were determined varies and is lowest for $A_h;A_h$ and $D_h;D_h$ translocations with high frequencies of configurations with a single interstitial chiasma that cannot be assigned with certainty to one breakpoint or the other (MENZEL, RICHMOND and DOUGHERTY

1985). A reviewer suggested that this uncertainty, coupled with sampling error, introduced so much error into the above analyses as to obscure the relationship between breakpoint location and dp-df frequency. (This is tantamount to assuming that 95% of the map locations are wrong.) In a subset of the data that included only breakpoints with an uncertainty of ≤1 cM, R^2 falls to less than 0.0. In all regressions, the coefficients of the independent variables were not significantly different from 0. In eight out of the 12 cases, the intercept was significant and ranged from 8.44 to 12.52% deficiencies. In every regression except one, the mean square for the residuals was larger than the mean square from the regression, frequently much larger. Therefore, this subset of the data likewise affords no evidence that distance of the breakpoint from the centromere governs frequency of dp-df transmission.

We examined dp-df frequencies involving breakpoints in the same arm. Examples of the following relationships were found:

1. The breakpoints are at significantly different positions, but the dp-df frequencies are similar (*9*R, *19*L, *21*R).

2. The breakpoint locations are not significantly different, but the dp-df frequencies are (*1*L, 2L, *3*L, *19*R).

3. Both breakpoints and dp-df frequencies are different, and the farther the breakpoint from the centromere, the higher the frequency of dp-dfs (as we originally expected) (*14*R).

4. Both breakpoints and dp-df frequencies are different, but the farther the breakpoint from the centromere, the *lower* the dp-df frequency (*16*R). It is tempting to postulate that these data reflect real differences in the organization of different arms, but we think it is more likely that they are only another manifestation of the independence of dp-df frequency and proportion of the arm that is deficient.

It has been postulated [*e.g.*, LIMA-DE-FARIA (1980)] that certain chromosome functions characteristically have proximal, distal, or medial locations. Translocations that interchanged equal proportions of chromosome arms would not disrupt the "field," according to this hypothesis, whereas those that had unmatched breakpoints (*i.e.*, one medial and one proximal or distal, or one proximal and one distal) would be more disruptive to functional relationships than equal-arm exchanges. If this concept were relevant to the transmission rate of dp-dfs, we would expect the lowest frequencies among the five translocations that have one distal and one proximal breakpoint (*T13;19 2925*, *T2;14 2B-1*, *T3;19 E20-7*, *T7;21 2790* and *T8;12 2778*). However, the frequencies of their ten adjacent-1 dp-dfs span the range of frequencies found in the entire sample.

We conclude that the positions of the breakpoints have no predictable relationship to the viability of the dp-dfs. Rather, the viability of each cytotype appears to be idiosyncratic.

Is the idiosyncratic frequency of a specific deficiency governed by the specific duplication with which it is associated? Data that bear directly on this question are sparse. However, in three instances, independent translocations involving the same two chromosomes have both their breakpoints at similar positions in the same arms (Table 4). In all three cases, the frequencies of each of the types of adjacent-1 cytotypes are rather similar in the two lines. The greatest disparity (25% *vs.* 16%), found for *dp17R; df9L* between lines *1036* and *6340*, is not significantly different ($P > 0.9$). On the other hand, two of the translocations have their breakpoints in the same chromosomes but at dissimilar positions. These lines are discordant in the frequencies of both types of dp-dfs, though the difference is significant only for H15. These meager data suggest that dosage interactions between specific chromosome regions do play a role in determining dp-df viability. It is unlikely that any of these interactions represents homoeologous dosage compensation such as occurs in compensating nullitetrasome combinations in wheat [*e.g.*, SEARS (1952, 1958)]. Only six of the 13 pairs of A_h and D_h homoeologues have been tentatively identified in cotton, on the basis of duplicate linkage groups, similar morphological traits of monosomes and telosomes, or both (ENDRIZZI, TURCOTTE and KOHEL 1985), but since two of the same-arm pairs of translocations in Table 4 involve two A_h chromosomes, the postulated interactions cannot represent interaction between homoeologues. None of the 56 translocations involves a pair of putative homoeologues.

Does chromosome damage at breakpoints affect recovery rate? It is conceivable that chromosome damage associated with the breakpoint has an effect on dosage sensitivity. However, all but one of the translocations are readily maintained as phenotypically normal, homozygous translocation lines, so recessive effects of damage can be dismissed. The exception, *T8;12 2778*, has a recessive mutation associated with the translocation that dwarfs the homozygote but does not prevent maintenance of the homozygous line (BROWN 1980) (M. Y. MENZEL and K. L. RICHMOND, unpublished data). Yet the *dp8;df12* cytotype from this translocation, which has the chromosome constitution *8, 8, 12,* 12^8, has one of the highest frequencies, and a homozygous dp-df (*8, 8,* 12^8, 12^8) that exhibits most of the recessive phenotype has been recovered from it (M. Y. MENZEL and K. L. RICHMOND, unpublished data). (The complementary *8,* 8^{12}, *12, 12* cytotype has never been recovered!) Thus there are no data to support the conjecture that chromatin damage at the breakpoint governs the dosage response.

TABLE 4

Frequencies of duplication-deficiencies from pairs of cotton translocations with both breakpoints in the same chromosomes (from Menzel *et al.* 1986)

Translocation and line		Estimated position of breakpoint (cM from centromere)		Frequency of adjacent-1 deficiencies for	
		Chr. A[a]	Chr. B[b]	Chr. A[a]	Chr. B[b]
T1R;16R	*2770*	54.26	69.16	0.00	0.00
	4672	44.12	69.16	2.50	0.00
T2R;8R	*1039*	0.00	0.00	10.00	0.00
	1058b	2.50	2.48	12.50	2.50
T9L;17R	*1036*	9.04	17.90	25.00	20.00
	6340	5.90	7.82	16.28	16.28
T15L;16R	*8-5Ga*	37.35	37.35	2.53	7.59
T15R;16R	*2767*	6.46	6.02	18.00	18.00

[a] "A" refers to the chromosome with the lower chromosome number.
[b] "B" refers to the chromosome with the higher chromosome number.

Are some chromosomes or chromosome arms inherently more sensitive to hemizygosity than others? It is conceivable that some cotton chromosomes contain regions that cannot be tolerated readily in hemizygous condition. Variation in dosage sensitivity is suggested by the fact that monosome lines have been established for only 15 of the 26 chromosomes (9 A_h and 6 D_h), and the monosomes that have been identified vary widely in their transmission rates [ENDRIZZI, TURCOTTE and KOHEL (1985) and see Table 5]. Moreover, monosomes for some chromosomes have arisen repeatedly, whereas others have been discovered only once (EDWARDS *et al.* 1980). Many additional spontaneous monosomic plants morphologically different from the 15 established lines have been observed by cotton workers but have failed to be transmitted. Since *G. hirsutum* is a cytologically diploidized allotetraploid, it could be postulated that the missing monosomes are chromosomes that contain genetically diploidized regions that are no longer compensated by homoeologous regions in the other genome. If this were true, dp-dfs deficient for the 15 "monosome" chromosomes should be more frequent (*i.e.*, more viable) than those deficient for the 11 "missing" chromosomes.

In 24 of the translocations, both chromosomes have monosomes. Among a total of 1045 plants analyzed from these lines, 195 adjacent-1 dp-dfs were found (18.6 ± (SD) 1.2%). In nine translocations, neither chromosome has a monosome. Among 603 plants analyzed, 79 adjacent-1 dp-dfs occurred (13.1 ± 1.4%). The difference between the two frequencies is highly significant ($\chi^2 = 8.128$, $P < 0.005$).

In the remaining 23 translocations, one chromosome has a monosome and the other does not. Among 1682 plants analyzed, 247 (14.7 ± 0.9%) adjacent-1 dp-dfs were deficient for part of a monosome chromosome, and 156 (9.3 ± 0.7%) for a missing chromosome. Again, the difference is highly significant

TABLE 5

Transmission rates of cotton monosomes compared with rate of recovery of duplication-deficiencies monosegmental for the same chromosome from progenies of heterozygous translocations × TM-1 (standard line)

Chromosome	Monosome transmission		Deficiency recovery		
	No. of plants	Percent monosomes[a]	No. of plants	No. of translocations	Range of dp-df frequency
A. Monosomes available					
H1	104	35 (33)	486	8	0–31
H2	121	45 (40)	391	8	0–25
H3	139	7	309	6	0–17
H4	173	49 (38)	273	3	0–23
H6	138	32 (37)	269	4	7–19
H7	128	21	318	6	4–19
H9	137	4	266	7	3–25
H10	119	23	260	4	2–10
H12	128	30	312	2	4–28
H16	133	7	212	3	0–18
H17	137	37 (21)	143	4	16–23
H18	127	43 (37)	44	1	9
H20		Very low	325	6	4–12
H22		Low	51	1	14
H25	128	32	65	2	10–17
B. Monosomes not available					
H5			235	5	0–15
H8			313	5	0–3
H11			419	6	9–28
H13			134	2	6–10
H14			370	5	1–21
H15			447	5	1–24
H19			547	8	0–26
H21			218	4	2–6
H23			116	2	7–13
H24			155	2	3–4
H26				0	

[a] After ENDRIZZI, TURCOTTE and KOHEL (1985), for progenies grown at Tucson, AZ [data from MALEK-HEDAYAT (1981)]. The numbers in parentheses are from BROWN and ENDRIZZI (1964) for progenies grown at College Station, TX.

TABLE 6

Frequencies of duplication-deficiencies monosegmental for the short (Sh) and long (Lo) arms of chromosomes lacking monosomes but having known monotelodisomes for the Lo arm (deficient for the Sh arm)

		Frequency of adjacent-1 deficiencies		
Telosome	Arm	Translocation	Line[a]	Percent of progeny
5 Lo	*5* Sh	*T5L;19L*	*C14-3*	15.2
	5 Lo	*T3R;5R*	*8-5Gb*	2.5
		T5R;12R	*SL18*	15.2
		T5R;23R	*2775a*	5.2
	Long *vs.* short arm, $\chi^2 = 0.345$, 1 d.f., NS			
14 Lo	*14* Sh	*T6L;14R*	*AZ-7*	1.1
		T2R;14R	*2B-1*	20.6
	14 Lo	*T14L;24R*	*2781*	5.6
		T1L;14L	*2780*	7.5
		T14L;23R	*2777*	5.2
	Long *vs.* short arm, $\chi^2 = 7.83$, 1 d.f., $0.01 > P > 0.005$			
15 Lo	*15* Sh	*T15R;16R*	*2767*	18.0
		T15R;20R	*SL15*	22.9
	15 Lo	*T4R;15L*	*1040*	9.3
		T15L;16R	*8-5Ga*	2.5
		T11L;15L	*1058a*	1.0
	Long *vs.* short arm, $\chi^2 = 28.19$, 1 d.f., $P < 0.005$			

[a] In order of the estimated distance of the breakpoint from the centromere (MENZEL, RICHMOND and DOUGHERTY 1985).

($\chi^2 = 20.10$, $P < 0.005$). These data support the hypothesis that the missing monosomes are chromosomes with regions that are not readily tolerated in hemizygous condition. (It follows, however, that some of them may be *more* readily tolerated in trisegmental condition.)

However, both groups of chromosomes (*i.e.*, with and without monosomes) are heterogeneous in their frequencies of deficiencies (Table 5). The transmission frequency of monosomes ranges from 4% for H9 to 49% for H4 and is unrelated to the genome to which the monosome belongs. When these frequencies are compared to frequencies of dp-dfs monosegmental for the same chromosomes, little relationship is seen. For example, H2, with a high monosome transmission rate, has translocations with deficiency frequencies for H2 ranging from 0.0 to 25.2%, whereas H9, with the lowest monosome transmission rate, has deficiency rates from 3.0 to 25.0%. Among chromosomes lacking monosomes, similarly wide ranges are found.

Thus the dp-df data afford only equivocal evidence for the hypothesis that monosomes have not been established for certain chromosomes because they are inherently intolerant of hemizygosity. H8, H21, and H24 are possible candidates, whereas H11 and H19 almost certainly do not fall in this category. In view of the wide range of dp-df frequencies for each chromosome, it is conceivable that other translocations could be generated that would yield more convenient dp-df frequencies even for H8, H21 and H24.

Telosomes have been established for the long arms (deficient for the short arms) of three chromosomes not represented by monosomes, H5, H14 and H15 (ENDRIZZI and RAMSAY 1979, 1980; ENDRIZZI, TURCOTTE and KOHEL 1985). The left (L) and right (R) arms of H5, H14, and H15 have been reconciled with the long (Lo) and short (Sh) arms defined by telosomes (M. Y. MENZEL and K. L. RICHMOND, unpublished data). For the two D_h chromosomes, short-arm deficiencies are significantly more frequent than long-arm deficiencies (Table 6); frequencies are not significantly different for H5.

We conclude that some cotton chromosomes and chromosome regions may be tolerated in hemizygous condition less readily than others, but their identification is not strongly supported by these data.

This work was supported by grant 84-CRCR-1-1383 from the Competitive Research Grants Office, United States Department of Agriculture.

LITERATURE CITED

BROWN, M. S., 1980 Identification of the chromosomes of *Gossypium hirsutum* L. by means of translocations. J. Hered. **71:** 266–274.

BROWN, M. S. and J. E. ENDRIZZI, 1964 The origin, fertility and transmission of monosomics in *Gossypium*. Am. J. Bot. **51:** 108–115.

BROWN, M. S., M. Y. MENZEL, C. A. HASENKAMPF and S. NAQI, 1981 Chromosome configurations and orientations in 58 heterozygous translocations in *Gossypium hirsutum*. J. Hered. **72:** 161–171.

CONTOLINI, C. S. and M. Y. MENZEL, 1987 Early development of duplication-deficiency ovules in *Gossypium hirsutum*. Crop Sci. **27:** 345–348.

EDWARDS, G. A., M. S. BROWN, G. A. NILES and S. A. NAQI, 1980 Monosomics of cotton. Crop Sci. **20:** 527–528.

ENDRIZZI, J. E., 1974 Alternate-1 and alternate-2 disjunctions in heterozygous reciprocal translocations. Genetics **77:** 55–60.

ENDRIZZI, J. E. and G. RAMSAY, 1979 Monosomes and telosomes for 18 of the 26 chromosomes of *Gossypium hirsutum*. Can. J. Genet. Cytol. **21:** 531–536.

ENDRIZZI, J. E. and G. RAMSAY, 1980 Identification of ten chromosome deficiencies in cotton. J. Hered. **71:** 45–48.

ENDRIZZI, J. E., D. T. RAY and A. C. GATHMAN, 1983 Centromere orientation of quadrivalents of heterozygous translocations and an autoploid of *Gossypium hirsutum* L. Genetics **105:** 723–731.

ENDRIZZI, J. E., E. L. TURCOTTE and R. J. KOHEL, 1985 Genetics, cytology, and evolution of *Gossypium*. Adv. Genet. **23:** 271–375.

LEWIS, K. R and B. JOHN, 1966 The co-orientation of non-homologous centromeres. Heredity **21:** 692–694.

LIMA-DE-FARIA, A., 1980 Classification of genes, rearrangements, and chromosomes according to the chromosome field. Hereditas **93:** 1–46.

MALEK-HEDAYAT, S., 1981 The relationship between seed weight and 13 monosomic and two monotelodisomic chromosomes in *Gossypium hirsutum*. M.S. thesis, University of Arizona, Tucson.

MENZEL, M. Y. and M. S. BROWN, 1952 Viable deficiency-duplications from a translocation in *Gossypium hirsutum*. Genetics **37:** 678–692.

MENZEL, M. Y. and M. S. BROWN, 1954 The tolerance of *Gossypium hirsutum* for deficiencies and duplications. Am. Nat. **78:** 407–418.

MENZEL, M. Y. and M. S. BROWN, 1978 Reciprocal chromosome translocations in *Gossypium hirsutum*. Arm location of breakpoints and recovery of duplication-deficiencies. J. Hered. **69:** 383–390.

MENZEL, M. Y. and K. L. RICHMOND, 1986 A revised map of chromosome 15 of *Gossypium hirsutum*. Can. J. Genet. Cytol. **28:** 272–277.

MENZEL, M. Y., K. L. RICHMOND and B. J. DOUGHERTY, 1985 A chromosome translocation breakpoint map of the *Gossypium hirsutum* genome. J. Hered. **76:** 406–414.

MENZEL, M. Y., C. A. HASENKAMPF, B. J. DOUGHERTY, K. L. RICHMOND and L. B. CAMPBELL, 1986 Characteristics of duplications and deficiencies from chromosome translocations in *Gossypium hirsutum*. J. Hered. **77:** 189–201.

RHOADES, M. M. and E. DEMPSEY, 1953 Cytogenetic studies of deficient-duplicate chromosomes derived from inversion heterozygotes in maize. Am. J. Bot. **40:** 405–424.

RICHARDS, G. K., 1983 Orientation behavior of chromosome multiples of interchange (reciprocal translocation) heterozygotes. Annu. Rev. Genet. **17:** 443–498.

SEARS, E. R., 1952 Homoeologous chromosomes in *Triticum aestivum*. Genetics **37:** 624.

SEARS, E. R., 1958 The aneuploids of common wheat. Proc. First Int. Wheat Genet. Symp. 221–229.

SNEDECOR, G. W. and W. G. COCHRAN, 1967 *Statistical Methods*, Ed. 6. pp. 199 ff. The Iowa State University Press, Ames, Iowa.

Communicating editor: M. R. HANSON