Table 33. Frequencies of X-chromosome inversions and of translocations between X and chromosomes 2 and 3 (Kaufmann 1946).

	Inversions in X		Translocations	
	Obs.	Expected	Obs.	Expected
2-break exchanges regions 1 to 19 in X	87	34.22	305	357.78
2-break exchanges one break in 20	53	24.90	142	170.10

rated by one or more turns of the coil (Kaufmann 1946). There was no tendency for new breaks to be clustered around the points of inversion in the delta-49 inversion stock used for part of the treatments. In a later report, treatment of the inversion heterozygote produced breaks at or near the original points of breakage. The distribution of breaks among the four limbs of chromosomes 2 and 3 from X-ray treatment as reported by Bauer et al. (1938) and Bauer (1939) and from nitrogen mustard treatments (Kaufmann et al. 1949) was essentially at random. At the higher dosage of X-rays (4,000r), the more complicated types of exchanges were more frequent than expected, as analyzed by Lea (1947).

Treatment of the female germ cells in Drosophila produced a much lower frequency of translocations (Glass 1956). At an average of about 2,000r, the frequency was about 6% in the progeny of treated males and only about 0.06% (one case) in those from treated females. Two possible reasons were offered: (1) the mature ♀ germ cells had not passed through meiosis (they were still diploid), (2) the chromosomes were farther apart and moved less.

Viability of interchange homozygotes

If interchanges are the result of mere exchanges of segments, one might expect the homozygotes to be viable. In Drosophila, less than half of them are fully viable. The others are lethal or lower than normal in viability or in fertility (Table 34).

Table 34. Viabilities of males and females heterozygous or homozygous for the same translocation in Drosophila (tabulated from Bridges and Brehme 1944).

	Homozygotes for translocations involving			Heterozygotes for translocations involving		
	X chrom.	Other chrom.	Total	X chrom. (males)	Other chrom.	Total
Number fully viable	7	24	31	9	53	62
" lethal	6	21	27	5	0	5
" semilethal or viable but sterile	6	8	14	15	0	15
Totals	19	53	72	29	53	82

Table 34 shows that male flies heterozygous for translocations involving the X also frequently have lower than normal viability, but heterozygotes for translocations involving the other chromosomes are fully viable. A probable explanation of this difference in viability in heterozygotes is the presence of a small deficiency or a recessive lethal

mutation at or near the break point, produced at the time of breakage. In heterozygotes, the effect of such a change in the X chromosome would not be covered by the Y, whereas a similar change in heterozygous females or in heterozygotes for translocations between the autosomes would be covered by the normal chromosomes. This also accounts for the lethality or lowered viability of homozygotes. Another observation suggesting the same explanation is that two 2-3 translocations, each of which was lethal when homozygous, gave a viable F_1 when crossed (Dobzhansky and Sturtevant 1931). Hoover (1938) reported deficiencies at the break points in a tandem inversion in Drosophila, but in general, cytological examination has shown detectable deficiencies only in a few cases.

In contrast to the behavior in Drosophila, most of the interchanges in plants are normal when homozygous. The probable reason for this difference is the presence in higher plants of a gametophyte screen against deficiencies and its absence in animals. The procedure in establishing interchange homozygotes in maize and barley has been to select the fertile plants in the self progeny of interchange heterozygotes, and test-cross them on standard normals. In maize, only two have not been established as homozygotes. One had a defective endosperm, the other a chlorophyll deficiency closely linked with the interchange. Of a group of 29 interchanges in barley, the one not established as a homozygote is associated with a recessive chlorophyll deficiency (Tuleen, 1960).

Homozygotes have been established also in Datura stramonium (Bergner et al. 1933, Blakeslee et al. 1940); in Triticum monococcum (Yamashita 1947), and in Pisum sativum (E. R. Sansome 1932, 1933).

Position effects

Several translocations in Drosophila have a dominant character completely linked with them, e.g. Baroid (Dobzhansky 1932), Pale translocation (Bridges 1923), and Variegated or Mottled eye color (Glass 1933). One possible explanation is that the new characters are the result of bringing genes together in new positions, i.e. a "position effect".

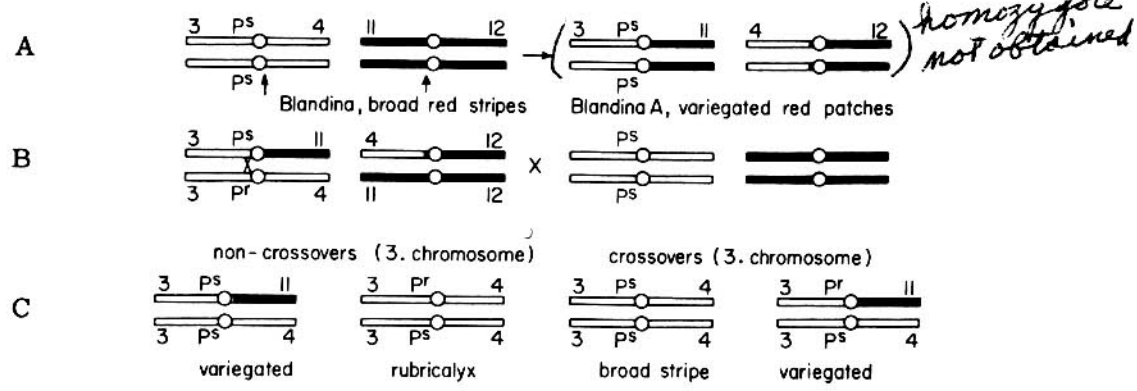

FIG. 26. Position effect as observed in Oenothera (based on the description by Catcheside, 1947).

A. An exchange of the 4. and .12 arms in Blandina which has broad red stripes on the calyx produced Blandina A with variegated red patches.

B. Blandina A/red calyx [P^s(A)/pr] crossed with Blandina (P^s). The crossover shown in the heterozygote produces the two types shown below on the right.

C. Constitution of the .3 chromosomes in the two non-crossover and the two crossover types. The transfer of P^s back to the normal 3.4 chromosome restored the broad red stripe phenotype (only one crossover type recognizable phenotypically).

The best-established example of position effect in plants is in Oenothera and involves the factors P^S (broad red and narrow green stripes on the sepals) and P^r (red or rubricalyx) as reported by Catcheside (1939, 1947). In normal O. blandina, P^S is in the 3. end of the 3.4 chromosome, but an interchange blandina A strain in which it is in the 3.11 chromosome has variegated patches of red in place of the broad red stripes, as shown in Fig. 26.

The interchange blandina A strain was crossed with a rubricalyx (P^r) strain and the F_1 backcrossed to the normal broad striped strain; as shown in Fig. 26B. Half of the progeny were expected to be variegated and half rubricalyx. Catcheside observed 712 of these two types and five with broad red stripes, the normal P^S phenotype. When checked, the five plants with broad red calyx stripes did not have the interchange. Hence, rather than mutations they were crossovers which transferred P^S back into the normal chromosome. Crossing over between P and the interchange point is indicated in Fig. 26B. The expected constitutions of the progeny for the chromosome carrying the P locus are shown in Fig. 26C. Only one of the crossovers was phenotypically recognizable. Further studies showed that when P^r crossed over into the 3.4 chromosome it resulted in a variegated phenotype. When P^r was transferred back to its original chromosome the phenotype also reverted. The various transfers and the number of each may be summarized as follows:

Kind of transfer (crossover)	Number	Genes involved	Phenotype, change from
3.4 (normal) to 3.11 (interchange)	17	P^S	striped to variegated
"	17	P^r	rubricalyx to variegated
3.11 (interchange) to 3.4 (normal)	17	P^S	variegated to striped
" "	17	P^r	variegated to rubricalyx
Total	68		

It is unusual for position effects to be regularly separable from the chromosomal change with which they are associated.

Position effects have not been recognized with certainty in translocations in other species of plants. In Datura, Blakeslee et al. (1940) stated that in their collection of over 90 prime types (homozygous chiefly for segmentally interchanged chromosomes) most were not distinguishable from normal plants but that a few were distinctly abnormal. They were not able to determine whether the abnormalities were due to completely linked genes, small deficiencies at the point or points of breakage, or to position effect.

Atypical growth of endosperm tissue visible as outgrowths and depressions in small areas on the surface of mature maize seeds have been described by Jones (1941). In seeds heterozygous for three independent endosperm markers (C, Pr, and Su), eleven mosaic areas for losses of these characters in pairs were observed. Interchanges could have initiated the paired loss of markers from different chromosomes. In later experiments, red areas and red brittle areas were observed on seeds from crosses of red aleurone (pr) brittle (bt) endosperm stocks with Purple Bt (Jones 1944). Some of these were paired with an outgrowth of tissue, others not. The interpretation was that these growth changes were associated with breakage and relocation of chromosome parts, and that this relocation stimulated growth activating regions (one between Bt and Pr) to increased growth.

The effects attributed to the Dissociation-Activator (Ds-Ac) system by McClintock (1953) may be considered as examples of a type of position effect.

In one study in maize, heterozygous and homozygous progenies of 13 interchanges, obtained by X-raying an inbred line, were compared with each other and with the inbred line (Roberts 1942). There were no conspicuous new characters, but small statistically significant differences in quantitative characters, date of first pollen, date of first silks, height, stalk diameter, leaf width, and leaf length were found. Of 138 comparisons, 42 were significant at the P = .01 level (Table 35).

Table 35. Frequencies of significant differences in quantitative characters in comparisons between homozygous and heterozygous interchange progenies and the original inbred C20 parent (Roberts 1942).

Change from normal C20 showed in	Date pollen + -*	Date silks + -*	Height plant + -	Diameter stalk + -	Width leaf + -	Length leaf + -	Total signif. changes + -	Total comparisons
homo. and hetero.	2	4	8	2	2	8	2 24	
homo. only	1 2	2	1	1 1	3	2	2 11	
hetero. only			1	1		1	1 2	
total	5	6	10	5	5	11	42	138

* later than inbred C20

As shown in Table 35, over half showed the difference in the homozygote and in the heterozygote. The magnitude of the effect in the heterozygote was intermediate. This suggests the effect was not due to a recessive, and also that it was additive. Most of the significant differences were in the direction of less vigor. The conclusion was that no striking position effects were found, but that "recessive mutations do not adequately account for all the changes found." Changes in quantitative characters produced by the treatment that produced the interchanges could explain the results. They may or may not have been linked with the interchange points.

Special types of interchanges

Pseudoisochromosomes

One type that has arisen in plants from radiation treatment of seeds (X_1) is that in which the exchange is between end segments of opposite arms of the members of one homologous pair, as shown in Fig. 27.

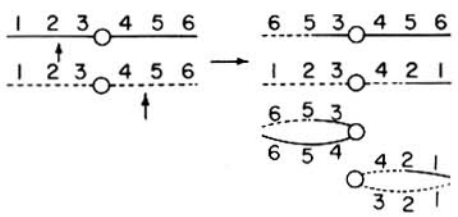

FIG. 27. The origin of a pair of pseudoisochromosomes by exchange of an end segment of one chromosome with the end segment of the opposite arm of its homologue. Transmission of both to a gamete is necessary for this type to be perpetuated. If the two pseudo-iso's pair, a crossover between the two breaks will produce a normal and an inverted chromosome.

The two ends of the resulting chromosomes are homologous and pair at meiosis as isochromosomes do, but the segments proximal to the centromere are not homologous. Hence they are termed "pseudo-isochromosomes."

Pseudo-isochromosomes have been described in barley (Caldecott and Smith 1952), maize (Morris 1955), and in oats (Koo 1958). Their structure has been confirmed at pachytene in maize (Morris 1955). Studies of their transmission have not been reported, but thus far none have

appeared in second generation cultures from irradiation. The only functional spores expected are those having both chromosomes. Crosses with normal pollen might secure their transmission through the female.

Interdependent rings

In Campanula a plant with two interdependent rings of four occurred in the progeny of a plant with a ring of eight chromosomes (Darlington and Gairdner 1937). In Oenothera there is one report of a plant with a ⊙ 4 ⊙ 6 which produced only two complexes whereas four would be expected (Emerson 1936). One way in which this may occur can be illustrated by assuming that a distal segment of every arm of four chromosomes is involved in an exchange with a distal segment of another of these four chromosomes, as described by Inman (1957) and shown in Fig. 28.

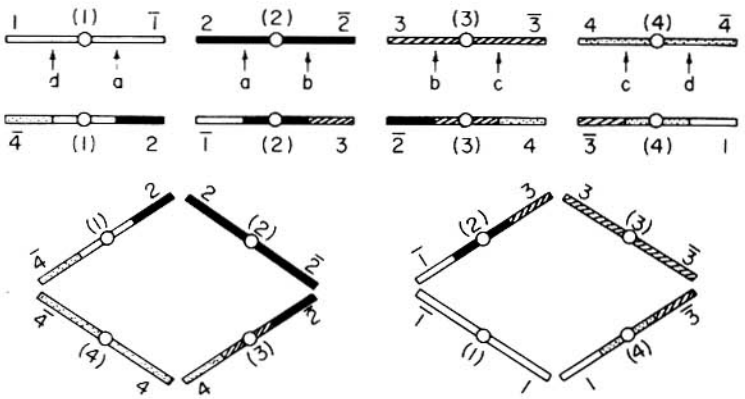

FIG. 28. A multiple series of four interchanges involving four non-homologues which will produce two interdependent rings of four chromosomes, based on the principle described and illustrated for 10 chromosomes by Inman, 1957. The homologue of one mid-segment (differential segment) is present in the other ring, hence there are only two viable combinations of chromosomes, not four.

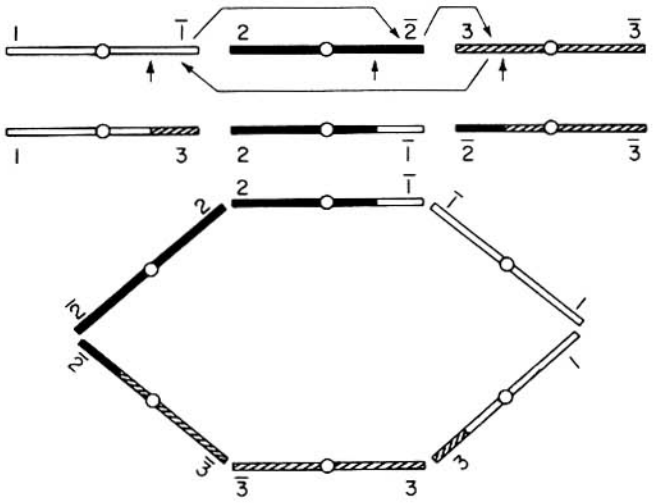

FIG. 29. Progressive or cyclic type of transpositions involving segments of three chromosomes. A ring of six chromosomes is expected in the heterozygote. The exchanges are not separable by crossing over.

The cross of the resulting multiple interchange stock with normal is expected to produce in F_1 2 ⊙ 4 in which the differential segments in one ring have their homologues in the other ring as shown in Fig. 28. Hence this F_1 will form only two viable types of spores. The same is true whenever an even number of chromosomes is involved in interchanges between every arm in the manner shown in Fig. 28. For example in corn, there would be 2 ⊙ 10. If one of these interchanges is omitted, or if every arm in a species with an odd number of chromosomes is involved, crosses with normal will produce individuals that have all the chromosomes in one ring at meiosis.

Cyclical or progressive translocation

Another type of change theoretically possible is one in which there are succes-

sive or progressive transpositions and substitutions of end segments as shown in Fig. 29.

This would be most likely where several breaks occurred simultaneously. Two cases have been found in Datura, and two in maize which may be of this type. In Drosophila, T(2:3)109 Sturtevant, has such a cyclical rearrangement in which terminal pieces of only two chromosomes, 2L, 2R and 3L are rearranged (Bridges and Brehme 1944, p. 197) as shown in Fig. 30.

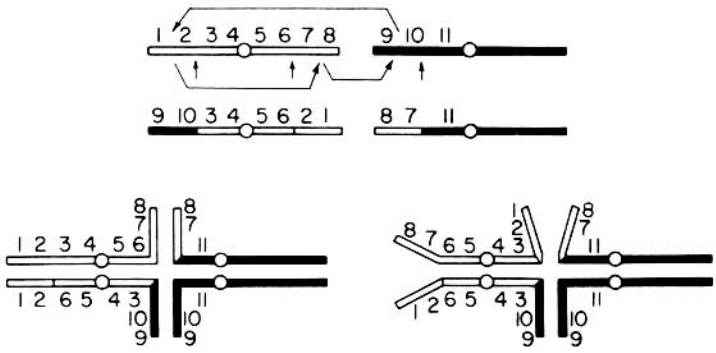

FIG. 30. Progressive or cyclic type of transpositions involving segments of two chromosomes, as described in Drosophila for T(2:3)109 (Lewis, DIS. 25 and Bridges and Brehme 1944). If homologous ends are associated in the heterozygote, the segment between the breaks in one chromosome is inverted in relation to its homologue as shown on the left. If homologous mid-segments are associated in proper order, the components of the ends of two adjacent arms of the cross are non-homologous (diagram on the right).

Note that there is a ⊙ 4 in the heterozygote but that the differential segment (between the two breaks in one chromosome, numbered 3 4 5 6) is inverted if the 1 2 ends are paired in pachytene.

Duplication-Deficiency interchange heterozygotes

This type of heterozygote may arise in the progeny of an interchange heterozygote if one of the interchanged segments is relatively short, as shown in Fig. 31A.

The a + d combination of chromosomes from the complex has a short deficiency and a longer duplication. In plants it may function through the female and produce a deficiency heterozygote as shown in Fig. 31B.

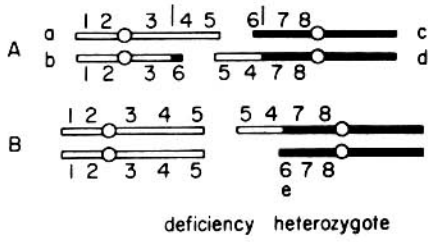

FIG. 31. A. Heterozygote for an interchange involving an exchange of segments of very unequal length. One of the Dp - Df spores, a + d, is functional, in higher plants usually only through the ♀. Interchanges of this type in maize show about 25% spore abortion.
B. Deficiency heterozygote of type used by Smith (1948) to locate genes.

If the deficiency includes the locus of a known recessive, the interchange heterozygote or the deficiency heterozygote when crossed as ♀ with the recessive ♂ will produce some recessive F_1 plants. This has been termed "pseudo-dominance." This furnishes a method of locating new genes, and of determining the location in the chromosomes of genes already placed. As an example, part of the data reported by Smith (1948) comparing the segregations in normal plants with those in a Df-Dp heterozygote in T. monococcum are shown in Table 36.

Table 36. Data from tests to locate recessive characters in T. monococcum by the use of duplication + deficiency, and normal stocks (Smith, 1948, from Table 3, p. 262, Bot. Gaz. 109, Univ. of Chicago Press).

Parent plants	Factor segregating	Total	Numbers in F_2 Dom.	Rec.	% rec.
normal	y	3090	2309	780	25
def.-dup.	y	322	260	62	19*
normal	g	1434	1064	370	26
def.-dup.	g	199	156	43	22
normal	e-1	5227	4447	780	15
def.-dup.	e-1	402	262	140	35**
normal	ar-2	1157	963	194	17
def.-dup.	ar-2	601	370	231	38**

y = yellow
g = greenbase
e-1 = early
ar-2 = argentia

* Significant deviations from the ratio in the progeny of the normal.

** Excess of recessives

Comparisons of the ratios in Table 36 for the same recessive in the normal and in the Df-Dp heterozygote show significant deviations for y and for e-1 and ar-2. For y there was a deficient ratio in the Dp-Df heterozygote which suggests y might have been in the duplicated segment, e.g. in the 5 4 segment (Fig. 31). For e-1 and ar-2, there was an excess of recessives in the progeny of the Dp-Df heterozygotes. This is expected if the genes were linked and in the remainder of the chromosome to which the 5 4 segment was attached, i.e. in the 7 8 segment. Had they been in the deficient segment, the F_1 would have been recessive. Smith suggested that segregation for factors in a third chromosome might be upset in a stock having an interchange between the normal chromosome in the Df-Dp stock shown in Fig. 31B and the third chromosome. The extent to which such stocks may be used remains to be determined.

The functioning of deficiency-duplication (Df-Dp) spores is common in chain-forming interchanges as in T1-6b in maize (Burnham 1932), although not limited to this type. If interchanges are being transferred to other inbred backgrounds, crosses using the interchange heterozygotes as the male parent will usually preclude the functioning of Df-Dp spores.

Studies of crossing over in duplication (plus Df?) heterozygotes derived from translocation heterozygotes have been reported in Drosophila. In one experiment a segment of chromosome 2 was described as being attached to the Y-chromosome. In a ♀ with two normal 2's and the duplicated segment on the Y, crossing over was reduced in the normal 2's in the region duplicated and in adjacent regions (Rhoades 1931). Other experiments were reported by Dobzhansky (1934). In one of these, Dp (1:2) from translocation (1:2) 7, the break in the X-chromosome was between rb at 7.5 and cv at 13.7. This terminal segment was transposed to a point beyond sp at or close to the end of chromosome 2. It may well have been a reciprocal exchange. In females with two normal X chromosomes and carrying the duplication attached to 2, crossing over at the extreme distal end of the X was reduced to 1/3 of normal, then was less reduced in adjacent regions until it became almost normal as v at 33.0 was reached. There was a slight decrease in crossing over in the region in 2 adjacent to the duplication (Dobzhansky 1934).

High sterility, high 3-1 segregation

In a strain of maize from Manchuria, Brink and Cooper (1932) reported plants with a chain of 4 chromosomes and 25% pollen abortion (M-sterile). When selfed or crossed

as ♀ with a normal stock the progeny showed a ratio of about 2 partially sterile : 1 normal (Table 37).

Table 37. Data on breeding behavior of the M-sterile heterozygote (25% pollen abortion).

	Partially sterile	Normal
M-sterile selfed, obs.	51**	23
expected (2:1)	49	25
M-sterile ♀ x N♂ obs.	30**	16
expected (2:1)	31	15
N x M-sterile ♂, obs.	145	154
expected (1:1)	149.5	149.5

** About half of these had over 40% aborted pollen, the others about 25%.

The partially sterile plants included a new class with much higher sterility, about 40%. Also, through the pollen the high-sterile class was missing and the ratio was about 1 25% sterile:1 normal.

Cytological study of the plants with 25% pollen abortion showed chain-of-four configurations at diakinesis and a T-shaped configuration at pachytene. Cytological study at late anaphase I showed that "high-sterile" plants had a high frequency of 9-11 segregations of the chromosomes. They assumed a simple translocation, but an exchange with one piece very short, as in Fig. 31A, would fit the results also. If an interchange is assumed the high-sterile plants should have resulted from fertilization with the gamete carrying a duplication and a short deficiency (e.g. the a + d chromosomes in Fig. 31A). No other case of such behavior in interchanges has been reported. Unfortunately this stock has been lost. A systematic check is needed of the chain-forming interchanges in maize.

In Pisum, Nilsson (1933, 1936) reported a ratio of fertile to partly sterile plants of about 1:2 for which no explanation has been reported. The homozygous type was not lethal. Heterozygosity for a gametophyte factor linked with the interchange point will explain deviations from the expected 1N: 1 heterozygous interchange ratio when the heterozygote is crossed as the ♂ parent on a normal stock, as in a 5-6 interchange in maize (Burnham, unpublished), and in Triticum monococcum (Yamashita 1952).

Interchanges between normal and supernumerary chromosomes

Interchanges between normal 'A' type and 'B' type chromosomes in maize are another source of deficiency-duplication gametes. Several of this type have been produced by X-rays (Roman 1947). Their breeding and cytological behavior have been described by Roman and Ullstrup (1952). The diagrams in Fig. 32 show the breakage positions and the resulting interchange heterozygote. The possible types of spores from the heterozygote shown in Fig. 32 are as follows:

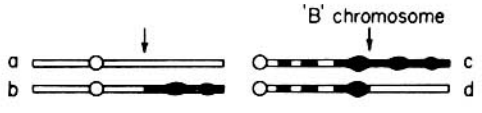

FIG. 32. Heterozygote for an interchange between a normal 'A' type and a supernumerary 'B' type chromosome in maize. In the microspores the 'B' chromosome and the interchange chromosome that has the 'B' centromere, chromosomes c and d, respectively in the diagram, undergo nondisjunction at the division of the generative cell to form the two sperms. As a result, in the spore which received the b + d chromosomes, one sperm is deficient for the transposed segment of the normal chromosome, the other has it in duplicate.

Kind of segregation	Spore types	Functional microspores: Tube nucleus	Sperm #1	Sperm #2
Alternate	a+c = N	a+c	a+c+c	a
	b+d = N (interchange)	b+d	b+d+d	b
Adj. 1	a+d = Dp*	-	-	-
	b+c = Df (abort.)	-	-	-
Adj. 2	a+b = Dp*	-	-	-
	c+d = Df (abort.)	-	-	-

* Hyperploid spores, unable to compete in the pollen

Only those spores deficient for a segment of the "A" chromosome would be expected to abort, i.e. b+c and c+d. If segregation were in a ratio of 2 alternate : 1 adjacent-1 : 1 adjacent-2; or 1 alternate : 1 adjacent-1 as in chains, spore abortion would be about 25%.

Through the ♀, the Dp or hyperploid combinations, a+d and a+b, would be expected to function in addition to the normal combinations, a+c and b+d. Through the pollen, only the normal combinations would be expected to function, but in one of these, the b+d combination, the d chromosome with the 'B' centromere frequently undergoes non-disjunction of sister chromatids at the second post-meiotic division, i.e. the division of the generative nucleus to form the two sperms. Hence one sperm in the b+d spore has two of these chromosomes, the other none. Thus one sperm is deficient for the translocated piece of the 'A' chromosome, the other has it duplicated. Since the first division of the microspores is normal, the tube nucleus has no duplication and the pollen-tubes are under no handicap in competition with microspores having the a+c combination of chromosomes. Genetic data indicate that the frequency of this non-disjunction of the chromosome with the 'B' centromere at the division of the generative nucleus varies from 90 to 100%. If a homozygous dominant A-B interchange heterozygote is crossed as ♂ on plants carrying a recessive marker in that segment, part of the F_1 progeny will be recessive, indicating a deficiency had been transmitted through the pollen. The behavior is illustrated by the results of reciprocal crosses between homozygous TB-4a Su Su and a normal sugary su su stock (Roman and Ullstrup 1952); and of a TB-7 heterozygote crossed on opaque glossy (o_2 gl), two linked genes on chromosome 7 (Table 38).

Table 38. Results of crosses with an A - B interchange: TB4a crossed reciprocally with su su.

	F_1 total seeds	No. of recessives in F_1	% rec.
homo. TB-4a Su Su x su su	1157	0	0
su su x homo. TB-4a Su Su	1791	929 su	51.9
$o_2$gl x TB-7/normal	63	0 o_2	0
		21 gl	33.3

The su seeds in F_1 show that the normal allele of su was in the interchanged segment of 4 in TB-4a. In TB-7, Gl was in the interchanged segment of 7, O_2 in the centromere

bearing segment of 7. Since the recessives appeared only when the interchange was used as the male parent, non-disjunction similar to that in the first division of the microsoore did not occur in the divisions to form the female gametophyte.

Since the sugary (su) seeds observed in F_1 in the cross of su su x TB-4a Su Su must have been fertilized by the deficient sperm, the eggs in the same embryo sacs should have been fertilized by the hyperploid sperm (two B^4 chromosomes and one 4^B). Examination of 24 plants from the su seeds showed that all had an extra B^4 chromosome as expected. Genetically they should have been Su Su su. When selfed these plants produced 6.4% su seeds in a total of 2181. This is a trisomic ratio, again indicating that su was in the transposed segment. The Su F_1 seeds from the cross of su su x TB4a should have come from the opposite type of fertilization, the hyperploid sperm fertilizing the endosperm nuclei, the deficient one the egg. Their embryos should be deficient. Of the 27 plants from Su seeds that were examined, 24 had no B^4 chromosome but only a normal 4 and a deficient 4^B and therefore might be expected to have about 50% pollen abortion and completely normal progeny in the next generation. Tests showed this to be true. The other three plants were heterozygous for the interchange and must have come from normal disjunction in the division of the generative nucleus.

The T-B interchanges are useful in locating genes, and in determining gene positions within the chromosomes. Some cytological checking must be done to maintain the stocks, since even the homozygote will produce hyperploids.

Pure breeding types with extra chromatin material

Blakeslee saw in the interchanges another method of producing pure breeding types with extra chromatin material. One of the methods described by Blakeslee, Bergner, and Avery (1933, 1936) depends on attaching the extra material to chromosomes which the plant cannot get along without. One of these will be described here. A prime type (PT6) was said to be characterized by a free .1 fragment and a 2 portion attached to an 11.12 chromosome, forming a 2 11.12 chromosome. From the heterozygote (upper portion of Fig. 33), the normal 1.2 chromosome plus 2 11.12 chromosome was established in homozygous condition as PT5 (Fig. 33).

In PT5, as shown in the figure, the 1. fragment has been eliminated and there were four doses of the 2 segment. This stock bred true for five generations and resembled closely the 2n + 2.2 type.

Since later evidence is against the occurrence of simple translocations, as assumed in the above description, the original PT6 was probably an interchange in which a long piece of the .2 arm exchanged positions with a very short segment of the .11 arm. In that case, the 2 11.12 chromosome from PT6 would be deficient for the short segment lost by 11.; also PT5 would be homozygous for that deficiency. This might account for differences between the phenotype of PT5 and that of a normal 2n+2.2 secondary trisomic.

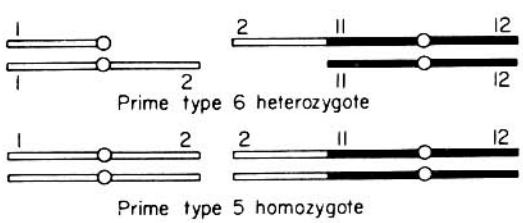

FIG. 33. Chromosomal constitution of the prime type 6 heterozygote in Datura from which the prime type 5 homozygote was established (based on the description by Blakeslee et al., 1936). Prime type 5 may have been an interchange of the type shown in Fig. 31A.

Two cases were described also in which lines with an extra chromosome pair and a phenotype similar to the 2n+2.2