some 1.2 the primary and one of its two secondaries were not transmitted, but the other secondary, sugarloaf, was transmitted. Its pollen tubes grew at about 2/3 of the normal rate.

Greater transmission of the slower growing ones was obtained also by grafting styles (Buchholz, Doak and Blakeslee 1932). Pollen from a 2n + 1 was applied to the stigma. A number of hours later they removed and discarded the portion of the style containing the advance groups of tubes (n) and grafted the upper part of the style with the stigma onto the lower part near the ovary.

If n + 1 pollen functions, the self progeny of trisomics should include tetrasomics. Some were established in Datura, but there seem to be no figures on frequencies.

The kinds of offspring observed in the progeny of the various types of trisomics will be considered next.

Observed breeding behavior of the various types

Primary trisomics

In Datura, it is possible to classify the various trisomics phenotypically, some as seedlings, others later. A summary of the results from selfing the primary trisomics

Table 53. Breeding behavior of the primary trisomics and of normal diploids. (From Blakeslee and Avery 1938 - Table 2, p. 322-323, Carnegie Inst. Wash. Pub. 501).

Prog. of 2n selfed	Type of trisomic	Progeny from selfing the 2n+1 types indicated in 2nd column: Total population	2n	Parental 2n+1	% parental 2n+1	Secondaries (no.) 1st arm	Secondaries (no.) 2nd arm	Unrelated 2n+1 (no.) Primaries	Unrelated 2n+1 (no.) Secondaries	Number 4n	Number n
6	1.2	2,049	1,780	213	10.40	1	5	27	-	23	-
-	3.4	2,089	1,634	452	21.64	-	-	1	-	1	1
3	5.6	2,367	1,591	725	30.63	2	-	24	2	18	-
-	7.8	2,080	1,865	208	10.00	-	-	6	-	1	-
4	9.10	2,160	1,454	686	31.76	1	-	13	-	3	-
-	11.12	2,228	1,716	491	22.04	2	-	14	1	1	1
6	13.14	2,033	1,451	538	26.46	-	-	29	1	7	1
4	15.16	2,278	1,788	458	20.11	1	-	21	-	2	-
4	17.18	2,140	1,565	558	26.07	1	-	11	-	2	2
1	19.20	4,758**	4,498	141	2.96	7	-	100	4	3	1
3	21.22	2,340	1,626	686	29.32	-	-	4	-	11	-
-	23.24	2,044	1,371	665	32.53	-	-	1	-	6	-
20,255*	Total	28,566	22,339	5,821	--	15	5	251	8	78	5
0.15	% 2n+1				22.08 avg.			0.76 avg.		0.26 avg.	
0.24	% 4n										

* Includes one secondary 19.19, 3 haploids and 48 tetraploids.

** Includes one 3n.

is in Table 53. The first column of that table is for the progeny of normal diploids.

Note in column 6 that the average frequency of primaries belonging to the parental type was 22.08% based on the entire population, with a range from 2.96% for the 19.20 chromosome to 32.53% for the 23.24 chromosome. There was no definite relation between frequency and chromosome length. The deviation from 50% is a result of the various factors mentioned above, their relative importance probably varying with the particular chromosome that is trisomic.

Although most of the trisomic progeny are of the parental type, trisomics for other chromosomes (unrelated trisomics) also occur as shown in the next to the last column in Table 53. The highest frequency of the latter was in the progeny of 2n + 19.20, a little more than 2%; but even in the total population, the frequency (0.76%) was higher than the occurrence of trisomics among the progeny of diploids, 0.15%. This suggests that the trisomics may have a somewhat higher rate of non-disjunction for the chromosomes that are not in triplicate, possibly a change in physiology of the plant has a general effect on chromosome disjunction. A similar behavior that occurs in wheat, unrelated monosomics occasionally appearing in the progeny of a monosomic, has been termed "univalent shift" (Person 1956).

As shown also in Table 53, a few secondary trisomics were found (less than one per thousand) in each case for one of the arms of the extra chromosome. Tetraploids appeared also, about three per thousand.

Secondary trisomics (2n + isochromosome)

The breeding behavior of the secondary trisomics in Datura is summarized in Table 54.

Table 54. Breeding behavior of the secondary trisomics (from Blakeslee and Avery 1938 - Table 2, p. 322-323, Carnegie Inst. Wash. Pub. 501).

		Progeny resulting from selfing									
	Parent	Total		Secondary		Rel. primary		Unrelated (no.)			
Chrom.	2n+	pop.	2n	number	%	number	%	Primary	Secondary	4n	n
1	1.1	1,956	1,857	48	2.45	47	2.40	4	-	-	-
1	2.2	1,857	1,424	332	17.88	75	4.04	6	1	18	1
2	3.3	2,409	2,145	146	6.06	87	3.61	18	1	11	-
3	5.5	2,256	1,400	702	31.12	120	5.32	17	1	12	-
3	6.6	2,338	1,762	403	17.24	140	5.99	1	2	29	-
4	7.7	2,762	1,931	764	27.66	51	1.85	4	-	9	1
5	9.9	2,237	1,659	359	16.05	187	8.36	25	1	2	1
5	10.10	1,998	1,361	559	27.98	48	2.40	24	-	1	-
6	11.11	2,271	1,827	397	17.48	27	1.19	9	-	8	-
7	13.13	2,035	1,704	205	10.07	114	5.60	7	-	2	-
7	14.14	2,372	1,812	468	19.73	71	2.99	17	-	-	1
8	15.15	2,249	1,668	457	20.32	76	3.38	13	-	32	-
9	17.17	2,244	1,808	275	12.25	146	6.51	7	-	7	1
10	19.19	2,864	1,996	850	29.68	2	0.07	15	-	-	-
	Total	31,848	24,354	5,965	18.73	1,191	3.84	167	6	131	5
	Avg. %				18.28			0.53			

Note in Table 54 that the 2n + 1 progeny of a secondary trisomic include the same secondary, the related primary trisomic (2n + 1. 2 is the related primary for the 2n + 1. 1 and 2n + 2. 2 secondaries); and also a few unrelated primaries. The percentages of secondary trisomics in the progeny varied from about 2% for the 1. 1 secondary to 31% for 5. 5. The percentages of related primaries ranged from . 07 to 8. 4%; with no obvious relationship, negative or otherwise to the transmission frequencies of the secondaries.

As shown in Table 52, column 1, pollen sterility was usually somewhat higher in the secondaries, as might be expected since spores with 11 chromosomes plus the isochromosome are deficient. The only exception is the primary Spinach which had a higher degree of sterility than its secondary, Divergent. For three others the difference was only 2 to 3 per cent. The average degree of pollen sterility for the primaries was 4. 9, and for the secondaries 11. 1 (omitting the exception). One of the primaries, Echinus (9. 10); and Mutilated, one of its secondaries (9. 9) were reported to have dimorphic pollen, roughly one half being filled with starch (Blakeslee and Avery 1938). As shown in Table 52, these trisomics have 3. 7 and 12. 5% of aborted pollen, respectively. According to Buchholtz's studies on pollen germination, neither is transmitted through the pollen, the former showing either burst pollen tubes or short ones, while the latter did not germinate.

Tetrasomics

Tetrasomics might be expected in the progeny of primary trisomics when n + 1 pollen is capable of functioning. They usually were less vigorous than the corresponding 2n + 1 and the characters of the trisomic were accentuated. Data on the breeding behavior of a tetrasomic for chromosome 8 (15. 16) are shown in Table 55.

Table 55. Breeding behavior in Datura stramonium of a tetrasomic, 2n + 2 or 2n + $(15.16)_2$ (from Blakeslee and Avery 1938, p. 322-323, Carnegie Inst. Wash. Pub. 501).

	Total	2n	Trisomic No.	Trisomic %	Tetrasomic No.	Tetrasomic %	Others
2n x tetrasomic	308	90	217	70.5	-		2n + 17.18
Tetrasomic x 2n	61	22	39	63.9	-		-
Tetrasomic selfed	69	19	34	49.3	15	21.7	2n + 15.15

As shown in Table 55, the tetrasomic did not breed true on selfing. In addition to the 2-2 disjunction from the tetrasome which results in n + 1 spores, there is considerable 3-1 disjunction which resulted in n + 2 and n spores as shown by the frequency of diploid offspring in crosses and selfs. The n + 2 spores did not function in pollen or ovules in those trials. The high proportion of n + 1 pollen probably accounts for its ability to function. In trisomics for this chromosome the n + 1 pollen tubes were slower growing than those with n (Table 52). The breeding behavior of tetrasomics for chromosomes which in n + 1 pollen from trisomics showed burst tubes was not reported.

If tetrasomics can be established and are sufficiently vigorous and fertile, they are an excellent means of producing progenies with a high frequency of trisomics.

Double trisomics

Since a root tip count indicating 2n + 2 may not be a tetrasomic, but a 2n + 1 + 1, in which there are two trisomes, it is interesting to note the breeding behavior in selfs of one such plant in Datura, as shown in Table 56.

Table 56. Breeding behavior in Datura of a double trisomic which was 2n + 5.6 + 9.10 (from Blakeslee and Avery 1938, p. 322-323, Carnegie Inst. Wash. Pub. 501).

Double trisomic (selfed)	Offspring								
	Total	2n	2n + 5.6		2n + 9.10		2n + 5.6 + 9.10		Others
			No.	(%)	No.	(%)	No.	(%)	
2n + 5.6 + 9.10	295	160	58	(19.7)	51	(17.3)	25	(8.5)	2*

* One 2n + 5.6 + 13.14 and one 2n + 23.24.

The frequency of double trisomics in the offspring as shown in Table 56, suggests that they were not disproportionately lower in viability. A comparison with Table 55 shows that the double trisomic (although neither was the chromosome in the tetrasome) had a much higher proportion of diploid offspring than did the tetrasomic. This might distinguish the quasi tetrasomic, 2n + 1 + 1, from the tetrasomic 2n + 2.

Telosomic trisomics

The breeding behaviors of a trisomic having one fragment chromosome, probably a telocentric (2n + 11.) and of a plant with a pair (2n + 2(.11)) are shown in Table 57.

Table 57. Breeding behavior of trisomic plants having one extra fragment (2n + 11.) and of plants having two extra fragments (2n + 2(11.)); Blakeslee and Avery, 1938, Table 6, p. 331, Carnegie Inst. Wash. Pub. 501.

	Offspring						
	Total	2n	(2n + 11.)		2n + 2(11.)		2n + 11.12 + .11
			No.	%	No.	%	
(2n + 11.) x 2n	74	45	29	39.2	-	-	-
(2n + 11.) selfed	143	69	63	44.1	11	7.7	-
2n + 2(11.) x 2n	64	20	44	68.8	-	-	-
2n + 2(11.) selfed	78	2	28	35.9	47	60.3	1

Note that the primary trisomic (last column) rarely occurred in the progeny of these 2n + fragment plants, indicating that disjunction of the 3 members of the group to the poles is not at random.

Table 58. Summary of chromosomal types found among progeny of the two tertiary trisomics, Pinched and Hedge (2n + 2.5 and 2n + 1.9 respectively) (Blakeslee and Avery 1938, Table 2, p. 322-323, Carnegie Inst. of Wash. Pub. 501). Percentages are in ( ).

Trisomic	Total plants	2n	Tertiary	Related primaries				Other
			2n+1.9	2n+1.2	2n+9.10	2n+1.1	2n+9.9	2n+1
2n + 1.9	2,489	2,072	369(14.8)	14(0.6)	25(1.0)	1	2	4*
			2n+2.5	2n+1.2	2n+5.6	2n+5.5		
2n + 2.5	2,089	1,436	601(28.8)	16(0.8)	18(0.9)	1		17**

* 3 kinds, plus two haploids.

** 9 kinds.

Tertiary trisomics

In a tertiary trisomic, the ends of the extra chromosome are homologous with the ends of two different chromosomes. Data on the chromosomal types found among the progeny of two tertiary trisomics are summarized in Table 58.

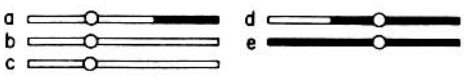

FIG. 49. Chromosomes of an interchange trisomic, type 1, Fig. 46. Chromosomes a, b and c are shown as forming the trivalent and d and e the bivalent.

Most of the offspring were diploids or parental tertiary trisomics. In addition the two related primaries as well as other primaries were found. That is, in the progeny of the 2n + 2.5 tertiary trisomic in which the ends of the extra chromosome are homologous with one end of 1.2 and one end of 5.6, these two primaries occur. Their frequency is relatively low (about 3%) but a little higher than for the unrelated primaries (about 1 to 2%).

The degree of pollen abortion in the tertiary and in the interchange trisomic depends on the kinds of segregation that occur in the group of five chromosomes. Methods of calculating expected amounts and of determining what occurs are outlined in what follows. The frequencies of the various possible configurations might be expected to vary depending on the relative lengths of the interchanged segments, and of the interchanged and non-interchanged segments. The one selected, for ease of calculation is an interchange trisomic (type 1 or 2 from Fig. 46 combined with normal chromosomes) in which a trivalent plus bivalent are assumed as shown in the diagram in Fig. 49.

Table 59. Kinds of spores with n + 1 and n chromosomes expected from the interchange trisomic shown in Fig. 49. The upper six combinations are duplicated by the lower six. In column 8 the spores that have n chromosomes and are viable (N) may have standard normal or interchanged (int.) chromosomes.

1	2	3	4	5	6	7	8
Kind of pairing	Contribution to n+1 from group of 3	group of 2	abort or N	Contribution to n from group of 3	group of 2	abort or N	Stand. or int.
a	a + c	d	N	b	d**	ab	
↕ c	or	e*	N		e	N	stand.
b	b + c	d**	ab	a	d	N	int.
		e	N		e**	ab	
a	a + b	d	N		d**	ab	
↕ b	or	e*	N	c	e	N	stand.
c	b + c	d**	ab	a	d	N	int.
		e	N		e**	ab	
b	a + b	d	N	c	d**	ab	
↕ a	or	e*	N		e	N	stand.
c	a + c	d	N	b	d**	ab	
		e*	N		e	N	stand.
Totals		10 N:2 ab			6 N:6 ab		4 stand. 2 int.

* tertiary combinations

** deficient combination, aborts

The trivalent and bivalent might be c-d-e plus a-b or a-b-c plus d-e. What the configurations would be and the kinds of segregation in Datura which shows directed segregation in a ⊙4 is not known. If random pairing within the trivalent and independent disjunction in the bivalent are assumed, the various kinds of n + 1 and n spores and their capacity to function might be as shown in Table 59.

The combinations in Table 59 were arrived at as follows. In column 1, the chromosomes that pair and disjoin are connected by the vertical ↕ . These pass to opposite poles and the third chromosome is assumed to be free to pass to either pole. For the first trivalent, a + c may go to one pole and b to the other, or b + c may go to one pole and a to the other. Each may be joined by d or e from the "bivalent". The n + 1 combinations are formed by combining columns 2 and 3, the n combinations by combining columns 5 and 6.

Only the eight combinations marked with a double asterisk in the above 24 are aborted. Since the percentage of abortion in the n + 1 and n classes is different, a change in the ratio of n + 1:n spores or deviations from random pairing will change the observed percentages of abortion. If pairing is random, the types of pairing and disjunction shown in column 1 of Table 59 will be equally frequent. The two normal chromosomes, b and c, in the trivalent might be expected to pair more frequently than they should due to chance, and a should pair with b as often as with c but with a lower frequency than b and c. If b and c always paired, n + 1 spores with the b and c chromosomes and n spores with a would be missing. Various proportions of the three types of pairing may be assumed, e.g. 4 b-c:1 a-b:1 a-c and these applied to the proper spore types (columns 2 + 3) and (5 + 6) expected from each type of pairing. The effect on sterility of changing the frequency of n + 1:n combinations may be determined by applying coefficients to the proper classes in columns 4 and 7. For example, if only 25% n + 1 is assumed; then the proportion of (n+1):(n) is 1:3. The percentages of spore abortion expected from various assumptions for an interchange trisomic and for a tertiary trisomic are summarized in Table 60.

Table 60. Summary of expected percentages of spore abortion in interchange and tertiary trisomics, also the kinds of 2n ofspring, with random and with preferential pairing.

Type of 2n + 1	Type of pairing	Ratio b-c:a-b:a-c pairing	ratio of n+1:n	ratio of normal: aborted among n+1 spores	ratio of normal: aborted among n spores	% spore abortion	2n offspring stand.: interch.
interchange*	random	1:1:1	1:1	5:1	3:3	33.3	2:1
	"	"	1:2	"	2(3:3)	38.9	"
	pref.	all:0:0	1:1	4:0	2:2	25.0	stand.
	"	"	1:2	"	2(2:2)	33.3	"
	pref.	4:1:1	1:1	11:1	6:6	29.2	10:2
	"	"	1:2	"	2(6:6)	36.1	"
tertiary	random	1:1:1	1:1	3:0	2:1	16.7	stand.
	"	"	1:2	"	2(2:1)	22.2	"
	pref.	all:0:0	1:1	all:0	all:0	0.0	"
	"	4:1:1	1:1	6:0	5:1	8.33	"
	"	"	1:2	"	2(5:1)	11.1	"

* two interchange chromosomes

As shown in Table 60, in an interchange trisomic, a ratio of 1 n+1:1n combined with random pairing in the trivalent would result in 33.3% spore abortion. With a 1:2 ratio of n+1:n, 38.9% would be expected. If entirely preferential (the two normals al-

ways paired), 25% is expected if the ratio of n+1:n is 1:1; 33.3% if it is 1:2. Other degrees of preferential pairing should give intermediate values. Certain combinations yield interchange combinations, others the tertiaries and one of the related primary trisomics. A tertiary trisomic resulting from an n + 1 gamete with the b, d and e chromosomes might be expected to throw the other primary trisomic.

A breeding test of interchange trisomic plants, e.g. from 3-1 disjunction type #1 or 2 in Fig. 46, should provide evidence on the type of pairing. One such test of 2n + 1 plants from T8-9a interchange heterozygotes in maize has been reported (Burnham, 1934). If pairing were at random, the 2n offspring would show a ratio of 2 normal : 1 semisterile (total of last column, Table 59). In a test through the pollen only 17.9% of semi-steriles was obtained. If preferential pairing is assumed between the two normal chromosomes to the extent of 4 (b-c) synapsis:1 (a-b):1 (a-c), 16.7% of semisterile plants would be expected, very close to the observed number. The expected sterility would then be 29.2% if the ratio of n + 1: n is 1:1; and 36.1 if it is 1:2. The observed sterility in this plant was 28% which fits the 1:1 ratio. The results indicate that preferential pairing does occur in the group of 5 chromosomes in the interchange trisomic.

Also as shown in Table 60, random pairing in a tertiary trisomic, combined with a ratio of 1n + 1:1 n, should result in 16.7% spore abortion. If entirely preferential (the two normal chromosomes always paired), no spore abortion is expected. If pairing is preferential to the same extent in a tertiary trisomic as for the first type from 8-9a (4:1:1) the corresponding values are 8.33% and 11.1% for ratios of 1:1 and 1:2 of n + 1:n spores respectively. Actually 9.9% abortion was observed in one such type from T8-9a (Burnham, 1930, 1934). It is probable that the degree of preferential pairing is dependent on the relative lengths of the interchanged and non-interchanged pieces.

Compensating trisomics

The breeding behavior of Nubbin, designated by Blakeslee as a compensating trisomic type is shown in Table 61. The data are from selfings of Nubbin or backcrosses as ♀ to normal.

Table 61. Types of progeny from Nubbin, a compensating 2n + 1 trisomic type in Datura (from Blakeslee, 1927, Table 1, p. 7. Ann. N. Y. Acad. Sci. 30).

			related primaries			secondary	related tertiary		unrelated primaries	Total
			Bk	Ec	R1		Ph	Hg		
Parent type	2n	Nb	5.6	9.10	1.2	2.2	2.5	1.9		
Nubbin (Nb)	668	424	9	14		1	58	36	10	1,220
%	54.8	34.8	0.7	1.1			4.8	3.0		

As shown in Table 61, the primary trisomic (R1) for the chromosome compensated for did not appear in the progeny of nubbin. Reference to Fig. 47 will show why this was true and also explain the occurrence of the Bk and Ec primaries and the related tertiaries. There were only about 1% of related primaries and 3 to 5% of tertiaries. The breeding behavior of these tertiaries is shown in Table 58.

Trisomics in other species

Maize

In maize, the ten primary trisomics were isolated by McClintock in the progeny of a triploid. The different ones were identified at prophase of the first post-meiotic divi-