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-

sion of the microspores by the presence of two identical chromosomes in the n + 1 spores (McClintock, 1929). They are numbered from 1 to 10, 1 being the longest chromosome, 10 the shortest. All have been available in separate stocks, except possibly that for chromosome 1, which was highly susceptible to smut in the original line. Only two of the primary trisomics in maize were strikingly different phenotypically from their diploid sibs in the original genetic stocks. Plants trisomic for chromosome 5 had shorter and broader leaves, while those for chromosome 7 had much narrower and stiffer leaves. Certain of the other trisomics tended to be a little shorter and a little less vigorous. No systematic study has been made of them in different uniform backgrounds, but in crosses with certain inbred lines, plants trisomic for chromosome 5 are difficult to distinguish from normals.

As in Datura, transmission through the eggs in maize is considerably less than 50% as shown by the data in Table 62.

Table 62. Data in maize on the relation between chromosome length and the frequency of trisomics in the progeny; also data on the frequency of univalents at meiosis (Einset, 1943, Table 3, p. 354, Genetics 28).

		Progeny of 2n + 1 x 2n		Microsporocytes		Microspores	
Chromosome	Relative length	Total no.	% 2n+1	Total no.	% with II + univ.	Total no.	% n+1
2	80	320	47	602	20	454	48
3	74	91	45	342	28	167	41
5	73	89	52	209	14	198	50
Avg.	76		48		21		46
6	60	155	38	109	28	109	34
7	56	80	41	246	26	193	50
8	57	191	31	267	40	245	36
Avg.	58		37		31		40
9	52	113	22	214	44	218	23
10	45	198	28*	672	43	299	34
Avg.	49		25		44		29

* Published data by McClintock and Hill (1931) on this chromosome showed 33% 2n + 1 in 124 individuals.

Although data for only three of the long chromosomes were reported, it is evident from Table 62 that the frequency of trisomics in the progeny was higher for the long chromosomes, and lower for the medium and short chromosomes. The frequency of univalent formation at metaphase I was lowest for the longer chromosomes; highest for the shorter ones. This may be interpreted to mean that the longer the chromosome the greater is the chance of its having crossovers sufficient to hold the three chromosomes together as a trivalent.

The relation between weight of seed and frequency of trisomics is shown in Table 63.

Table 63. Data on the relation between weight of seed and the frequency of trisomics in maize (Einset, 1942).

Chromosome number	Light		Medium		Heavy		Total
	Total number	% 2n+1	Total number	% 2n+1	Total number	% 2n+1	% 2n+1
2	73	84	107	51	99	18	48
3	43	86	52	52	82	7	40
5	24	58	28	71	37	32	52
6	30	77	42	12	31	10	30
7	16	63	23	39	19	21	40
8	56	54	61	41	74	5	31
9	13	46	24	71	76	3	22
10	66	50	72	19	60	15	28
Total for all	321	67	393	41	460	12	37

Transmission through the pollen in maize trisomics

From the cross of 2n x 2n + 1 (chromosome 10), McClintock and Hill (1931) found five (2n + 1) plants in a total of 349, or 1.4%. They established a tetrasomic for this chromosome, but it was a much shorter, weaker plant. Rhoades (1933a) reported no trisomic plants in a population of 1,845 from a similar cross involving the trisomic for chromosome 5.

In crosses involving a tertiary trisomic in which the extra chromosome consisted of a piece of 9 plus a piece of 8, Burnham (1934) found about 1% transmission through the pollen.

Barley

The seven barley, Hordeum vulgare, chromosomes have been numbered from 1 to 7 based on morphology and the linkage groups have been renumbered to correspond (Hagberg and Tjio, 1950; Burnham and Hagberg, 1956; Ramage, Burnham and Hagberg, 1961). Trisomics found in the progeny of interchange heterozygotes 1-2, 1-5, 1-6, 1-7, 2-4 and 3-7 in the Mars variety of spring barley were established by Ramage (1955). Some were tertiary types and others interchange trisomics. Primaries appeared among their progenies. Tsuchiya (1958, 1960) established the 7 primary trisomics in the progeny of a triploid crossed with H. spontaneum, a wild winter barley. Seed fertility in these ranged from 63 to 88%, considerably higher than in those established by Ramage, although Ramage was able to increase the fertility of certain trisomics in the Mars variety by selection. Transmission frequency and fertility were also higher in the H. spontaneum trisomics. Several of the trisomics are readily distinguished from each other and from their diploid sibs, in leaf and stem characters, and growth habit. Differences in leaf size and shape are shown by several primary and tertiary trisomics in cultures established by Ramage.

The trisomic for chromosome 2 has long, narrow, light-green leaves which droop, that for 4 has short, wide leaves, and that for 5 has narrow, dark-green leaves. Trisomics for 6 do not have very distinctive characters as seedlings. The

characteristics of the trisomics in H. spontaneum as described by Tsuchiya (1948, 1960) indicate differences in seed size and shape and other characters sufficient to distinguish all the trisomics.

Tomato

In the tomato, Lesley (1928, 1932)was able to isolate 9 of the 12 primary trisomics from the progeny of 3n x 2n plants and added two more in 1932. Although these were in a dwarf variety with determinate growth, they were more or less distinct in foliage characteristics and growth habit. They were much more difficult to recognize in hybrids.

The trisomics were re-isolated by Rick and Barton (1954) using as the source triploid plants of San Marzano, a variety with indeterminate growth. They are maintained by backcrossing to a diploid line of San Marzano, made homozygous by doubling a haploid.

The chromosomes in the normal complement have been numbered from 1 to 12 based on their pachytene lengths (Barton, 1950). The corresponding 12 primary trisomic lines have been identified; and designated by the number corresponding to pachytene length and morphology, i.e. Triplo-1, Triplo-2 etc. Each of the twelve types is readily distinguishable from the diploid sibs and from each other in the field, less easily in the greenhouse. There are differences in growth habit, internode length, leaf color, leaf shape and size, flower type, fruit shape and size which characterize the different trisomics. There is a tendency for the characters of different organs to be affected in a similar fashion. Fertility is greatly decreased in the trisomics, ranging from 3.3 seeds per fruit to 18.5; the normal diploid having 53.3. Triplo-1 was completely sterile in the field, but set seed well in the greenhouse. Many of the Triplo-9 seedlings lost their meristems in the cotyledon stage or at the 1- or 2-leaf stage.

Table 64. Transmission frequencies of the tomato trisomics (from Rick and Barton, 1954, Table 3, p. 652, Genetics 39).

Chromosome	Frequency in progenies from (2n+1) x 2n			Frequency in progeny from (2n+1) selfed		
	Total plants identified	2n + 1 Number	%	Total plants identified	2n + 1 Number	%
1	439	20	4.6	-	-	-
2*	409	18	4.4	193	16	8.3
3	661	7	1.1	-	-	-
4	311	77	24.8	467	146	31.3
5	598	133	22.2	344	88	25.6
6	224	1	0.4	-	-	-
7	593	88	14.8	294	53	18.0
8	717	156	21.8	772	193	25.0
9	517	86	16.6	423	70	16.5
10	666	133	20.0	237	55	23.2
11	415	61	14.7	627	116	18.5
12	476	75	15.8	300	52	17.3
Avg. %			13.4**			20.4

* This chromosome is associated with the nucleolus.

** The average is 17.2 if 1, 3 and 6 are omitted, to be comparable with the selfs.

The frequencies of trisomics in the progeny from self pollinations and in crosses with normal males are shown in Table 64.

Based on the data in Table 64, the transmission of n + 1 through the female ranges from 0.4% to about 25%. The frequency was in general somewhat higher in the self progeny of trisomics, but no data were reported on the two having the lowest transmission through the ♀. Their explanation for the higher frequencies among the selfs was that those stocks were highly heterozygous, whereas the others were from crosses within the San Marzano variety. Lesley compared the transmission frequencies through the pollen and through the ovules for two trisomics, as shown in Table 65.

Table 65. Data on transmission of trisomics through the pollen and through the ovules in tomato (from Lesley, 1928, Table 7, p. 33, Genetics 13).

	2n + 1 as ♀		2n + 1 as ♂	
Cross	Total plants	% 2n + 1	Total plants	% 2n + 1
Triplo-A crossed with 2n	316	24*	43	0
Triplo-A selfed	47	23		
Triplo-B crossed with 2n	83	27	90	23*
Triplo-B selfed	92	37		
Triplo-C crossed with 2n	-	-	52	10

* One 2n + 1 plant was not the parental 2n + 1.

The data in Table 65 show a high transmission frequency through the pollen for one trisomic, none for the other one tested. No tetrasomic plants were reported among any of the self progeny from these same trisomics.

For four of the chromosomes, Lesley and Lesley (1929) reported mutants which had 25 chromosomes, but the extra one was a fragment equal to about half the length of one chromosome, probably one arm plus the centromere (telocentric). As in Datura, their related primaries rarely occurred among their progeny (see Table 57).

Crepis and other species

In Crepis capillaris, five of the six trisomic types were identified cytologically (Babcock and Nawaschin, 1930). The sixth, for the shortest chromosome, was thought to be inviable or occurred only rarely. Levitsky (1940) found trisomics in the progeny of interchanges in C. capillaris. The four trisomics for C. tectorum were established and described by Gerassimova (1940). They differed from normals in type of growth and in leaf characters.

Trisomics have been isolated in stocks, Matthiola incana, some of which may have been primaries, others 2n + fragment types (Frost, 1927). Other examples are: snapdragon, Antirrhinum majus (Propach, 1935); rye, Secale cereale (Takagi, 1935), Pisum sativum (Sutton, 1939), Oenothera (Emerson, 1936a, Renner, 1949, Catcheside, 1954) and Nicotiana sylvestris (Goodspeed and Avery 1939). Those for spinach, Spinacia oleracea are shown in Fig. 50 (Ellis and Janick 1960).

Those in Pisum were noted first as off-type plants in the progeny of chromosomal interchanges. O. blandina has 7 II of chromosomes but three of them are involved in

interchanges if compared with O. hookeri, a race with 7 pairs selected as a standard normal race (see Chapter 5). Many different trisomics are possible in the progeny of multiple interchange heterozygotes such as Oenothera.

Trisomics in cotton, wheat and tobacco which are polyploids will be discussed in Chapter 8.

Drosophila melanogaster

Triplo-IV and haplo-IV individuals have been reported in Drosophila (Bridges, 1921). Non-random segregation was reported in triplo-IV females (Sturtevant 1936). In the stock having the X chromosomes attached at the centromere end (attached-X, actually an isochromosome), the females are XXY (Morgan, 1938a). They may be considered as a modified trisomic. There are also stocks in which the females are XXY but the X chromosomes are not attached. Only rarely do triplo-X flies survive (Bridges and Brehme, 1944).

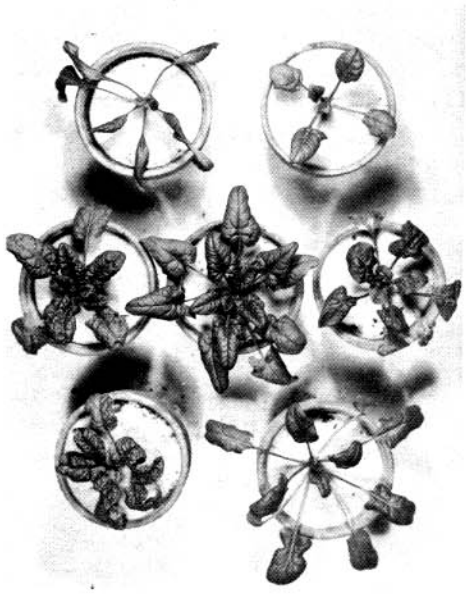

FIG. 50. The six primary trisomics of spinach, Spinacia oleracea. The normal 2n (Long Standing Bloomsdale variety) is in the center.
Top row: curled, reflex (sexchromosome)
Middle row: wild, normal diploid, oxtongue
Lower row: savoy, star.
(modified from Ellis and Janick, 1960, Fig. 3, p. 213, American Journal of Botany 47).

Man

Trisomics have been reported in man. Mongoloid individuals are trisomic for a particular autosome (Lejeune et al. 1959, and Jacobs et al. 1959). An individual that was mongoloid and also had the Klinefelter's syndrome had the extra autosome and was also XXY (Ford et al. 1959). Other subjects with genetic defects have been shown to be trisomic for a D_1 chromosome (Patau et al. 1961). A ♀ with gonadal dysgenesis had only one X chromosome (Tjio et al. 1959).

Genetic ratios

Genetic ratios in trisomic individuals are a means of locating genes and of establishing the independence of the linkage groups.

Primary trisomics

Since there is one trivalent (a group of three homologues) in a primary trisomic, the genetic ratios for factors that are located on these chromosomes will be very different from the ratios for genes on any of the other bivalent chromosomes. In a 2n + telocentric, the ratios for genes located in the arm that is trisomic will be modified. The ratios are modified still further by the low transmission of n + 1 through the pollen. The primary trisomic stocks, therefore, have been used in several species to determine the linkage group to which a genetic marker belongs, to identify the specific chromosome that carries it, and the 2n + telocentric or isochromosome has been used to determine the arm in which it is located. A trisomic may have the following genotypes for a particular locus, Aa as follows: AAA, AAa, Aaa, and aaa, referred to as triplex, duplex,