

Those underlined are higher in frequency than expected if disjunction were random. Also note that the lower chromosome numbers are relatively much more frequent than are the high numbers; although both are higher than expected. Chromosome lagging and subsequent loss have caused a shift to the lower chromosome numbers, while the tendency to go together to one pole in a larger group increases the frequency of the spores with higher numbers as well as those with the lower numbers. The end result is that both are still in excess of expectation, although the excess in the lower numbers is much greater and extends over a wider range of numbers than in the higher ones.

Fertility

In general, autotriploids are highly sterile, but in Spinacia oleracea they are described as having normal seed set (Janick and Stevenson 1955).

In triploid Datura, 50 to 60% of the pollen grains are filled, with considerable variation in size among them. Disintegration among the remainder begins soon after the first division of the microspore nucleus. The cells with intermediate numbers are supposedly the ones which abort, although this is probably not entirely a question of number. If the 17-, 18-, and 19- chromosome spores abort, 38% of abortion would be expected; while if the 16- and 20- chromosome classes are added, 58% would be expected. Of the full grains at maturity, 15% or less germinated; and nearly 2/3 of these pollen tubes burst at or near the stigma, leaving about 3% that behaved normally. As described previously (chapter 6), many of the $n + 1$ grains in trisomics are normal in appearance but will not germinate or will produce pollen tubes that burst. Studies of seed development and of chromosome number in the progeny of triploids also were reported (Satina et al., 1938). In the cross of $3n \times 2n$ Datura, 79% of the seeds were small, 21% of normal size or only a little smaller. In the normal diploid $\times 3n$ cross, the corresponding figures were 13 and 87%. There was an average of 61 seeds per capsule in the $3n \times 2n$ cross, the normal being 300 or more. As the seeds developed some had endosperm without an embryo, some the reverse, and others had abnormal embryos. Of 401 seedlings only 285 reached the stage at which they could be classified as to chromosome number and numbers of trivalents present. The results are in Table 76.

Table 76. Chromosome types in progeny of $3n \times 2n$ Datura (from Satina et al., 1938, Table 2, pp. 599, Amer. Jour. Bot. 25).

Total No. of plants	<u>$2n$</u>	<u>$2n + 1$</u>	<u>$2n + 1 + 1$</u>	<u>$2n + 1 + 1 + 1$</u>
285	58	138	79	10

All the primary trisomics except that for chromosome 19.20 were found in the $2n + 1$ progeny. Certain primaries showed delayed germination, the range being 3 to 258 days, whereas the diploids germinated in 3-12 days. The smaller seeds produced a higher percentage of $2n + 1$. In this experiment, no $3n$ plants were found in the progeny; but in others in which $3n$ plants were selfed over 2% of $4n$ plants were obtained.

Autotetraploids

Origin and occurrence

One of the new types which appeared in 1916 among the offspring obtained by selfing normal Datura stramonium was one with broad leaves and large flowers. This plant bred true on selfing but failed to set seed when crossed with normals (see Avery et al. 1959).

It was referred to as "New Species". Belling discovered it was a tetraploid in 1920. Sectors that are tetraploid may arise in a diploid. If at some somatic cell division the chromosomes divide but the nucleus fails to divide, a restitution nucleus results with its chromosome number doubled. Theoretically this may occur at any nuclear division, in somatic tissue, or in meiotic or post-meiotic divisions. For example, in Datura, $2n$ plants with tetraploid sectors or whole branches have been reported (Blakeslee and Belling 1924a, Avery et al. 1959). This writer observed in corn one spore-mother cell with 16 univalents and two pairs at diakinesis of meiosis.

If chromosome doubling occurs immediately following fertilization, the individual may have the doubled chromosome number in all its cells. If doubling occurs later, only certain sectors will have the doubled number. In general, the later the doubling, the smaller the sector; but differing rates of growth of diploid and tetraploid tissues may modify this. If a tetraploid sector includes ♀ and ♂ germinal tissue, there is a chance that the progeny may include a few tetraploids, especially if the species has perfect flowers and is naturally selfed. If the sector is small, there is a greater chance that the $2n$ eggs will be fertilized by n pollen, since $2n$ pollen rarely competes successfully with n pollen. One way to circumvent this competition has been to select the larger pollen grains under a microscope and use them in pollination. A horse-hair mounted in a dissecting needle handle has been used for the purpose of picking up the $2n$ pollen grains. The progeny from these pollinations are triploids. Chance doubling at the time of division of the generative nucleus in the microspores in seed plants would also avoid this competition, since the tube nucleus formed by the first division would have the n number.

Where polyploids have arisen spontaneously from diploid parents of known genotypes, it may be possible to determine at what stage chromosome doubling occurred, or at least to narrow the field of possibilities. In Datura, a tetraploid with the constitution PPpp AAAa arose in the progeny of the cross ppAA x PPaa (Blakeslee et al. 1923). Either a gamete with the doubled chromosome number from each parent produced this, or doubling occurred immediately following fertilization. Since the former would require the functioning of $2n$ pollen in competition with n pollen, and since no spontaneous triploids have been found in Datura, doubling following fertilization is the more likely explanation.

Another tetraploid (PPpp AAAA) was found in the self progeny of Pp Aa. In this case Blakeslee, et al. stated that doubling could not have occurred before reduction. A very small tetraploid sector on such a plant could form a Pp AA gamete, or this combination might have occurred during reduction; but even then such a gamete would not be likely to meet another like itself. Doubling probably occurred following fertilization for the same reasons as previously stated.

Chromosome doubling has been produced by various chemical and physical agents (see Chapter 9).

A few tetraploids have been found in maize in the progeny of $2n$ ♀ x $4n$ ♂, supposedly from a $4n$ sector or from unreduced cells in the female parent. This method has been used by Bauman (1961) to produce hybrid tetraploids. Colchicine, heat or other treatments applied to the $2n$ ♀, also increases the number of cells with doubled chromosome number.

Tetraploids have been produced in corn also by using pollen from $4n$ plants on plants with the asynaptic (as) or elongate character (el) as ♀. In asynaptic plants most of the chromosomes are present as univalents at diakinesis and metaphase I in ♂ and ♀. In elongate plants, the chromosomes are uncoiled at meiosis (Rhoades 1956). In the ♂ disjunction is normal but there is variable pollen abortion. In both mutants there is a high frequency of gametes with the unreduced chromosome number as well as aneuploid

and n numbers. In pollinations of these stocks and of normal stocks by pollen from $4n$, most of the seeds on the ears are triploids and are shriveled. The few plump grains on the ears are mostly $4n$ (Rhoades 1953), although some are $3n$ (Bauman 1961).

When doubling occurs in heterozygotes, segregation will occur in the polyploid progeny and selection will be possible in succeeding generations. If the original plant had been heterozygous for linked genes, and doubling had occurred in somatic tissue, crossing over would add to the number of possible new combinations.

Cytology

The configuration at diplotene of meiosis in autotetraploids may be a chain or string of four chromosomes, a $\odot 4$, a cross-shaped configuration, a trivalent plus univalent, or two bivalents.

The expected frequencies of the various kinds of possible associations of the members of a quadrivalent have been calculated for mean chiasma numbers per quadrivalent of 1 to 6 formed at random between the four chromosomes (Durrant 1960). The maximum frequency of two bivalents approaches 10%, but the average expectation is much less.

At meiosis in $4n$ corn, Randolph (1935) found the chromosomes arranged in quadrivalent and bivalent groups mainly; usually 7 IV + 6 II, 8 IV + 4 II, or 9 IV + 2 II. Trivalent + univalent formation was observed eleven times in 402 metaphases. At anaphase I: in 14 cells disjunction to the two poles was 20 - 20, in six 19 - 21 and one 18 - 22. Of 348 figures at anaphase I or early telophase, there were 13 with one lagging univalent and two with two lagging univalents. At the first microspore division Randolph found 16 spores with 20 chromosomes, five with 19, two with 18, four with 21, and one with 22 chromosomes. Several reports on the chromosome numbers of the progeny of corn plants with 40 chromosomes are summarized in Table 77.

Table 77. Numbers of chromosomes in progeny of 40-chromosome maize plants as reported in four studies.

Chromosome number														Total	Reference
20	36	37	38	39	40	41	42	43	44	45	46	47			
		1	3	6	27	12	5							54	Randolph 1935
	4	1	36	43	261	73	8	3						429	Kadam 1944
2	2	1	6	4	57	12	11	1	2	1	0	1		100	El-Ghawas 1955
			3	8	50	13								74	Catcheside 1956

About 60 percent of the progeny of 40-chromosome plants had 40 chromosomes. Certain of them might not have had four homologues of each chromosome; since $4n - 1 + 1$ will still have 40 as the total. Of the 57 40-chromosome plants that El-Ghawas analyzed, 48 had only quadrivalents and bivalents. The others had III + I, or several univalents but none had the configurations expected if a plant had been $4n - 1 + 1$. Using the frequency of 39-chromosome plants as the frequency of $2n - 1$ gametes and 41 chromosome plants as the frequency of $2n + 1$ gametes, he calculated the expectancy of $4n - 1 + 1$ plants as about 5 per thousand. Catcheside reported two plants believed to be of this type.

Fertility

In *Datura* the tetraploid showed 3.6 to 7.9% pollen abortion. In maize autotetraploids there was no increase in pollen abortion, but fertility on the ears was reduced by 5 to 20%. Lines differing in fertility could be established by selection. Some tetraploid lines in maize were self-sterile, according to Fischer (1941). Self-sterile x self-sterile lines produced highly fertile F_1 lines. F_2 populations were mostly self-sterile, unimodal or weakly bimodal. Backcrosses to self-sterile plants showed bimodal distribution. Fischer also found cross-incompatibility between certain stocks. Certain stocks which were self-fertile as the female parents were cross-sterile as males; others were self- and cross-sterile when used as the female parent in crosses, but were cross-fertile when used as the male parent. The original diploid lines showed no such behavior, and diploids that appeared as maternals in the progeny had normal fertility. This suggests that the incompatibilities were the result of a change in genic balance.

Gilles and Randolph (1951) reported some success in selection for higher seed-set over a period of 10 years in a tetraploid stock produced by crossing two tetraploid lines each of which originated from a hybrid between different inbreds. Quadrivalent frequencies in plants from the original ear for the lines and in plants at the end of selection for the ten years are shown in Table 78.

Table 78. Frequency of cells with different numbers of quadrivalents in tetraploid corn, before and after selection for higher fertility (from Gilles and Randolph, 1951, Table 1, p. 15, Amer. Jour. Bot. 38).

4n from	No. of quadrivalents						Total no. of cells	% of cells with 8-10 IV	Average no.	
	10	9	8	7	6	5			Quadri-valents	pairs
1937 seed	52	199	138	35	26	-	450	86	8.47	1.6
1947 seed	-	56	181	144	63	11	455	52	7.46	2.5

The data show a shift from higher to lower numbers of quadrivalents, and a corresponding shift from lower to higher numbers of bivalents. In a stock related to the one used by Gilles, Kadam (1944) found that 57% of the cells had 8, 9 or 10 quadrivalents. Hence, selection for higher seed set was accompanied by a higher frequency of bivalent pairing. They suggested that the original stock may have been heterozygous for a gene or genes that affect the frequency of quadrivalents. They also reported that fertility showed great seasonal variation indicating high sensitivity to various environmental variations that resulted in poorly filled ears.

Table 79. Kinds of frequencies of the various chromosome associations in autotetraploid *B. campestris* in the C_1 and C_{19} generations. (From Table 1, p. 387, Zeit. f. Vererbung. Bd 90, Springer-Verlag).

Generation	No. of cells	Quadrivalents		Trivalents		Bivalents		Univalents		Mean no. chiasmata per cell
		r*	m*	r*	m	r	m	r	m	
C_1	40	2-7	3.95	0-1	0.15	6-16	11.68	0-2	0.40	36.2
C_{19}	50	0-5	1.68	0-4	0.74	9-20	14.98	0-4	1.10	36.4
<u>2n</u>										18.3

* r = range, m = mean

Table 80. Number of cells with different numbers of multivalents. (From Table 2, p. 387, and Table 4, p. 389, Zeit. f. Vererbung. Bd 90).

Gener- ation										Mean no. per cell	% stainable pollen	No. seeds per <u>siliqua</u>	
	<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>			<u>range</u>	<u>mean</u>
C ₁	0	0	4	5	18	10	2	1	0	4.10 ± 0.17	92.6	0-3	1.5
C ₁₉	7	11	8	9	9	5	1	0	0	2.42 ± 0.22	90.2	10-21	16.8
												for 2 <u>n</u> , 13.8	

Data on the effectiveness of selection for fertility in autotetraploids of the turnip, *Brassica campestris* var. *Toria*, produced by colchicine treatment have been reported by Swaminathan and Sulbha (1959). Their data on the cytological configurations in the first and 19th generations after treatment are summarized in Tables 79 and 80.

As shown in Table 80, fertility measured by the number of seeds per siliqua was greatly improved in the 19th generation. This was associated with a higher frequency of bivalents and a lower frequency of multivalents as shown in Table 79 and 80. The mean number of chiasmata per cell remained about the same.

The data in these tables suggest a possible relationship between increased fertility and a lower frequency of multivalents.

Tetraploids of common flax varieties, Redwood and Bison, had only 2 to 3 seeds per boll as compared with 7 to 8 in the diploid. Yields per acre were only 30 to 40% of those of diploids (Ross and Boyes 1946). Masima (1945) reported only 10 to 28% fertility in *L. angustifolium*.

Dactylis glomerata, a natural polyploid, shows a high frequency of multivalents but seed production is completely normal (Brix and Quadt, 1953). Hence lower fertility is not necessarily a concomitant of multivalent formation. Some other factor which can be removed by selection must influence fertility, at least in certain species.

Maternal diploids

A phenomenon corresponding to haploidy in diploid species occurs also in autopolyploids. From a tetraploid, there are occasional diploid offspring which usually have whatever distinctive markers were carried by the female parent. From crosses between tetraploids in maize, using genetic markers for identification, Randolph and Fischer (1939) reported 23 such maternal diploids in a population of 17,165 individuals or a ratio of about 1:750. Chromosome counts on 20 of these showed 15 with 20 chromosomes, one with 21, three with 22, and one with 24 chromosomes. All were highly self-fertile and had normal pollen. Two were observed by El-Ghawas (1955) in a total of 100 plants (Table 77). Nilsson (1939) has reported diploid derivatives from an autopolyploid form of *Oenothera lamarckiana*. In tomatoes, after several generations from an autotetraploid, 11 of the 34 lines checked were diploids (Quadt 1955). In other species, the shift is so frequent that the autopolyploid condition cannot be maintained, e.g. *Eruca sativa* (Rajan, et al. 1950), and *Vicia villosa* (Hertsch, 1951).

Fertile "haploids" have appeared also in the progeny of natural polyploids. Bolton and Greenshields (1950) and Stanford and Clement (1958), have reported 16-chromosome plants showing mostly bivalents in alfalfa (*Medicago sativa*); whereas the normal is 32. Plants with 24 chromosomes have been found in the tetraploid (2n = 48) potato. Hougas and Peloquin (1958) have used them in genetic and breeding studies. These indicate that

the evolutionary trend may not always be from lower to higher numbers, and that autopolyploids may give rise directly to fertile diploids.

Polyploidy in animals

As pointed out earlier, polyploidy in sexually reproducing animals is rare. The reason given usually is that the chromosome balance for sex determination may be upset in the progeny of autopolyploids. This need not be true. Varying doses of X chromosomes and autosomes modify the sex expression in Drosophila, but not in Bombyx mori (silkworm), see Chapter 10, pages 279-280.

Most of the polyploids that have become established in animals in nature reproduce parthenogenetically. For example in the snout-beetles (Curculionidae), of 18 parthenogenetic species, only one was diploid, the others $3n$, $4n$, or $5n$ (Suomalainen 1954).

Triploid rabbits have been produced by colchicine treatment at the moment of fertilization (Haggqvist and Bane 1950). Of 7 young, three (1 ♀, 2 ♂) lived nearly a year, four died at 8 weeks or before. They noted that the erythrocytes and sperms in the ♂ were larger in size. Melander (1950) reported on the cytology of a male. Some mitoses were triploid and regular but others appeared to be irregular. In mice, $3n$ and $4n$ zygotes were reported after abnormal temperature treatment at an early stage. Higher, but different numbers of chromosomes were observed in cells of bone marrow and testicles.

In stickleback fishes there is one report of induced triploids that were vigorous and required less oxygen (Swarup 1959). (cf. Bungenborg deJong 1957, polyploidy in animals).

Haploids and monploids

The term "haploid", as used here, refers to individuals with the gametic number, but they may have arisen from a diploid or a polyploid. The term "monoploid" is used only for those that arise from a diploid and hence possess a single genome.

Origin and occurrence

The first monploids in a flowering plant species were observed in Datura stramonium. They occurred after exposure of young buds of diploids to cold (Belling and Blakeslee 1922). They were obtained also after prolonged exposure to low temperatures (Blakeslee et al. 1927), and after temperatures of 40° - 50° C applied immediately after pollination in corn (Randolph 1932). Monploids have been found among the progeny of interspecific or wide crosses, e.g. in the cross of Solanum nigrum x S. luteum (Jørgenson, 1928), and in the cross of Datura stramonium x D. ferox (Belling and Blakeslee 1927). Five were observed in over 3,000 plants from the cross of Crepis capillaris ($n = 3$) x C. tectorum ($n = 4$) (Hollingshead 1930).

Haploids may arise through development of the egg without fertilization, either through parthenogenesis or through pseudogamy (stimulation of development of the egg by pollination without fertilization or by fertilization of the primary endosperm nucleus only). In species having endosperm in the mature seed, the importance of fertilization to produce endosperm is obvious, but it may be equally important in initiating embryo development in other species. Randolph (unpublished data cited by Einset 1943) found a frequency of about 1 in 2,000 in untreated corn, with a range from 0 to about 6 per 1,000. The frequency is higher in certain stocks than in others when crossed with the same pollen parents; also frequencies differ when the same female parent is crossed with dif-