"Shift"

Somewhat different from the behavior described above are the interspecific crosses which fail to give segregation of the parental types in F_2 or later generations. No chromosome doubling has occurred. The explanation offered by Darlington (1928) is based on allosyndetic pairing. For example, Biffen (1916) reported no segregation for chaff color in the progeny of Rivet, a variety of Triticum turgidum with grey chaff crossed with T. polonicum having white chaff. Almost 100,000 plants were grown up to F_6 from 20 F_1 plants of that cross.

An explanation based on Darlington's suggestion is the following: in T. polonicum W_1 and W_2, suppressors of the grey-chaff characters, are assumed to be carried on different chromosomes that pair allosyndetically in the F_1 i.e. $\frac{W_1}{W_2}\ \frac{w_1}{w_2}$. All the resulting gametes have Ww and no segregation of grey-chaff color would be expected. To explain the unexpected pairing, it is possible that these two chromosomes of T. polonicum are more nearly homologous than either is with the corresponding chromosomes in T. turgidum.

As another example, the cross of Triticum polonicum (n = 14) with T. durum (n = 14), a cross which Aase reported formed 14 II or as few as 12 II, plus 4 I, segregated in F_2 in a ratio of one long glume: two intermediate: ~~two~~ short but the long-glumed types were shorter than those in the T. polonicum parent (Engledow 1920, 1923). This segregation may be explained in a similar manner, except that in addition to a major factor pair for ~~awn~~ length there are dominant short modifers contributed by the T. durum parent. The following genotypic and pairing scheme is a modification of that proposed by Darlington (1928).

T. polonicum x T. durum

L (long glume)
d_1 alleles of D
d_2

1 (short glume)
D_1 (short glume in one genome)
D_2 (short glume in second genome)

$$\frac{L}{1}\quad\frac{D_1}{D_2}\quad\frac{d_1}{d_2}$$

Here, glume length will segregate in a 1:2:1 ratio, but every gamete gets one of the dominant D modifiers, as a result of the pairing of chromosomes from different genomes. Hence, none of the plants would have glumes as long as those of T. polonicum. Only if pairing occurred between D and d would the LL d_1d_1 d_2d_2 genotype be produced.

Aneuploidy in allopolyploids

Progeny with chromosome numbers above and below the normal somatic number have been reported in a number of allopolyploid species. In general, the trisomics do not differ as much morphologically as do the trisomics from diploid species. In contrast with diploids, monosomic (2n - 1) plants usually can be established in polyploids, and in some instances nullisomics (lacking one pair) may be viable.

Types having an isochromosome or a telocentric chromosome have been found also, i.e. monosomic plus iso or monosomic plus telo; and nullisomic plus iso or nullisomic

plus telo. These and the monosomics and nullisomics will be discussed here, reference being made to the trisomics (2n + 1) and tetrasomics (2n + 2) whenever the studies on them are related.

The first report of monosomics in Nicotiana tabacum, was by Clausen and Goodspeed (1926) who described two plants with 47 chromosomes (2n -1). The first monosomics and nullisomics in wheat, Triticum vulgare (n = 21) were reported in studies of certain speltoid types (Winge 1924, Huskins 1928, Nishiyama 1928 and others), see page 234. Nullisomics and monosomics have been reported in oats also (Philp 1935, 1938, Costa-Rodrigues 1954, and McGinnis and Taylor 1961). An occasional monosomic plant has been reported in maize (McClintock 1929b, and Einset 1943). As expected in a diploid, the deficient spores in maize were abortive and all the progeny had the normal chromosome number. The only exception to this is the report of nullisomics in the progeny of certain lines of diploid Godetia. (Håkansson, 1943a, Hiorth 1948). The explanation offered was that by unequal interchange, the essential portions of one chromosome were transferred to others. Cytological study confirmed the presence of translocations.

Aneuploids in *Nicotiana tabacum*

The monosomics in N. tabacum will be discussed first, since they illustrate the general principles as to their cytological and genetical behavior. In 1944, Clausen and Cameron reported the isolation of 24 different N. tabacum monosomics believed to represent the complete set of possible primary types. They are designated haplo-A, haplo-B, etc. Monosomics appeared spontaneously in the offspring of a normal plant, in the progeny of backcrosses of [(N. tabacum (n = 24) x N. sylvestris (n = 12)] x N. tabacum (Olmo 1935), in the offspring of other monosomics, and in the progeny of asynaptic N. tabacum (called pale sterile) x normal. The latter source has the advantage of greater uniformity of genetic background which makes for easier identification of the types; and also permits the isolation of certain monosomics by plan. For example, a pale-sterile asynaptic plant crossed with a normal plant homozygous for a recessive gene will produce a few plants in F_1 which show the recessive and which must be monosomic at least for this chromosome. They may be monosomic for other chromosomes also.

Monosomic stocks are maintained by crossing monosomic ♀ x standard normal (purpurea) male which insures a uniform genetic background and also that the monosomic chromosome comes from the standard normal stock. The univalent chromosome in such crosses always comes from the male parent.

Description

The monosomics in N. tabacum differ from each other and from the normal in a complex of characters including corolla, calyx and capsule size, and size of plant, rate of development, leaf shape, intensity of chlorophyll and other characters. The monosomics are not as easy to recognize as are the trisomics of Datura stramonium or of Nicotiana sylvestris (Goodspeed and Avery 1939), each of which has a single basic genome of only 12 chromosomes. This might be expected, since the addition of one chromosome to a basic set of 12 represents a greater change in balance than the loss of one in 24 in the allopolyploid N. tabacum.

Meiotic behavior

The normal configuration at diakinesis in a monosomic N. tabacum plant is a univalent in addition to the pairs (23 II + I), but a trivalent from the association of the univalent with a non-homologue (22 II + III), or the failure of association (non-conjunction)

of one or more of the bivalents (22 II + 3 I, 21 II + 5 I) may occur also. In haplo-D and haplo-S about 25% of trivalent formation and about 20% of non-conjunction were reported. Trivalent association is rare in other monosomics, but the frequency of non-conjunction varies from about 5% to 25% or more. This may give rise to other monosomics in the progeny of a particular monosomic.

Chromosome disjunction is such that about 75% of the microspores in a monosomic carry 23 chromosomes and 25% carry 24 chromosomes. Frequent lagging of the univalent with the formation of micronuclei appears to be the cause of this deviation from 50%. However, the frequency of (n-1) may vary for different chromosomes, as shown above.

Spore abortion

A few of the monosomics had low percentages of completely aborted pollen, 3 to 22%, while the remainder had 62 to 86%. Normal plants had about 3%. Those monosomics with the lower percentages of completely aborted pollen had an additional class which was distinguished from normal by smaller size, or shrunken contents. The aborted and the smaller, shrunken pollen grains probably are the 23-chromosome (n - 1) spores.

Ovule abortion also shows a considerable range, from about 16% to 87%, without close agreement with the degree of pollen abortion.

Breeding behavior

The progeny of different monosomics crossed as ♀ with normal males include variable percentages of monosomics ranging from about 5 to 82%. Four monosomics had 70 to 82% of monosomic progeny, six others had 40 to 60%, four had 20 to 40% and the other ten had 5 to 20%. Hence part of the 23-chromosome spores do not abort. For "fluted" corolla (monosomic F), female transmission was 59.5% (Clausen and Goodspeed 1926).

Transmission of n-1 through the ♂ should produce some nullisomic offspring. If these zygotes occur in Nicotiana, they do not survive.

Exceptional progeny

Certain monosomics have given rise to lines showing variegation of flower color probably through formation of ring chromosome types which are unstable and carry the gene for color (Clausen 1930, Stino 1940) (see page 29 for a description of the behavior of ring chromosomes). In addition, fragment types, and also the corresponding trisomics may appear. The characteristics of the monosomic and its corresponding trisomic frequently differ from the normal in opposite directions. For example haplo-F and haplo-N are small flowered while triplo-F and triplo-N are large flowered; haplo-C on the other hand is large-flowered while triplo-C is small-flowered.

Identification of monosomics in relation to the basic genomes

As mentioned earlier, Clausen (1928) presented evidence that N. tabacum has the genomes of N. tomentosa and N. sylvestris. Crosses of the various N. tabacum monosomics with each species were used to identify the chromosomes belonging to each genome. For example, in the cross of N. tabacum monosomic with sylvestris, the parental gametes for the monosomic offspring are 12 + 11 for the n-1 gamete from the ♀ parent and 12 from the N. sylvestris ♂. If the missing chromosome in the n-1 gamete belongs to the N. sylvestris subgenome, i.e. 12t + 11s, the modal pairing will be 11 II + 13 univalents; if it is from the N. tomentosa subgenome, i.e. 11t + 12s, it will be 12 II + 11 univalents. In the former the 13 I are from 12t + 1s chromosome; in the latter the 11 I are all from N. tomentosa.

They have thus identified the 24 monosomics, finding that the chromosomes in the N. tomentosa subgenome range from small to large while those in the N. sylvestris subgenome range from medium small to large. At least two chromsomes are attached to the nucleolus, but only one has been identified.

Use of monosomics in locating genes

If the dominant allele is carried by the monosomic stocks, plants with the recessive character are crossed as ♂ on each of the 24 monosomics. All the 2n-1 offspring of these crosses are expected to receive their univalent chromosome from the ♂ or disomic parent. Hence, in one of the 24 crosses that gene will be carried by the chromosome present only as a univalent in the monosomic ♀ parent. The monosomic offspring of that cross, the critical one, will be recessive since they received this chromosome from the ♂ . The disomic sibs and all the F_1's of the crosses with the other monosomics should show the dominant character and segregate 3:1 in F_2. The cross may be represented as follows, the genotype of the critical monosomic being represented as A0 or a0*:

Description	Corresponding genotypes
P_1 = monosomic (dominant) x recessive	AO x aa
F_1 = disomic (dominant) and monosomic (recessive)	Aa and aO.

If on the other hand, the monosomics carry the recessive allele of the character being tested, the monosomic F_1's of the critical cross as well as the others will have the dominant character as shown below. Backcross or F_2 progeny will identify the critical cross. The cross may be represented as follows:

Description	Corresponding genotypes
P_1 monosomic (recessive) x dominant	P_1 = aO x AA
F_1 disomic (dominant) and monosomic (dominant)	F_1 = Aa and AO

The expected classes in F_2 from the monosomic F_1 are shown in the following checkerboard square:

♀ \ ♂	n=A	n-1=O
n=A	1 AA	2 AO
n-1=O	3 AO	4 OO

In this tabulation, cells 2 and 3 are monosomic, and cell number 4 is nullisomic.

The only F_2 offspring not carrying at least one dominant are the nullisomics (cell #4, in the above tabulation) and since in N. tabacum these do not survive, this F_2 does not have any recessive offspring. The F_2 phenotypic results will be the same regardless of the transmission frequency of monosomics. As we will see later, in wheat and in oats

* The O is used to indicate the missing member of the pair, following the usage in Drosophila, e.g. an XO male; and Kuspira and Unrau (1950) for monosomics and nullisomics in wheat.

the nullisomics may survive, thus furnishing information on the phenotype produced in the absence of the dominant allele.

By 1944, a total of 18 factors in N. tabacum had been placed to chromosome by this method, 9 in each genome. For the hairy filament and yellow burley characters, each determined by duplicate genes, one gene was found in one genome, one in the other. One of the critical crosses for the yellow burley character is summarized here:

	Phenotypes	Genotypes
P_1	haplo-B (green) x yellow burley	$\underline{Yb_1}O \quad \underline{Yb_2} \quad \underline{Yb_2} \times \underline{yb_1} \quad \underline{yb_1} \quad \underline{yb_2} \quad \underline{yb_2}$
F_1	diplo-B (green) and haplo-B (green)	$\underline{Yb_1} \quad \underline{yb_1}\ \underline{Yb_2} \quad \underline{yb_2}$ and $\underline{yb_1}O \quad \underline{Yb_2} \quad \underline{yb_2}$
F_2	76 green: 6 yellow 66 green: 23 yellow	↓ ↓
ratios:	15:1 3:1	seg. 15:1 3:1

The different ratio in F_2 from the haplo-B F_1's indicates that one of the yb factors is in that chromosome. In the above representation of the cross, the B chromosome arbitrarily is assumed to carry yb_1. By selfing and selecting for green in the F_2 progeny segregating 3:1 it is possible to isolate easily a yb_1yb_1 Yb_2Yb_2 tester stock. By a similar procedure the Yb_1Yb_1 yb_2yb_2 stock might be established.

The behavior of aneuploids in wheat differs in several respects from that in Nicotiana, and will be discussed next.

Aneuploids in wheat, *Triticum vulgare*

Monosomics

SOURCES. Sears (1939) reported monosomic plants and other off-types among the progeny of a haploid crossed with normal T. vulgare. The haploid occurred in the progeny of crosses between rye and a variety of spring wheat known as Chinese, a variety which gives a higher percentage of wheat-rye hybrids than do most varieties of wheat. Nullisomics and trisomics appeared among the progeny obtained from selfing the monosomics. Tetrasomics appeared in the self progeny of the trisomics. Monosomics also appear in the progeny of hybrids between species differing in chromosome number backcrossed to the parent with the higher number, e.g. (T. vulgare, 21 II x T. dicoccum, 14 II) x 21 II was used by Matsumura (1940) to establish monosomics and nullisomics for the chromosomes in the D genome.

Nullisomic -3B plants are partially asynaptic and were used as another source of monosomics. A recessive desynaptic gene in wheat reported by Li et al. (1945) would be another good source. By introducing it into a variety by several backcrosses and establishing the recessive stock, monosomics for that variety could be produced. If recessive marker genes were available, monosomics for those particular chromosomes could be produced.

Monosomics arise occasionally in the progeny of normal T. vulgare varieties. Cytological study shows a small percentage of irregular chromosome behavior at meiosis in all varieties, but some have a higher percentage than others; also the percentage is often higher in hybrids, and in varieties descended from species crosses (Powers 1932, Semeniuk 1947). In breeding work it has been possible to select for greater chromosome stability (Love 1939).

DESCRIPTION. The monosomics for the most part do not differ greatly from normal plants, nor from each other. However, the differences may be accentuated under poor growing conditions. In the variety Chinese, plants that are monosomic for chromosome 5D (18) are at least seven to ten days later than their normal sibs. Monosomic 5A (9) shows the heterozygous speltoid effect, i.e. thicker glumes, and lax, tapering heads (see page 234). Others may show minor differences. For most of them the 2n-1 plants can be identified only by a cytological count of the chromosomes at meiosis and the presence of a univalent. Occasional plants may be disomic for the chromosome that was univalent in the original monosomic parent, but monosomic for a different chromosome. This must be detected in studies using monosomics. Differences in plant morphology that do occur in the monosomics are accentuated in the corresponding nullisomic. For example, nullisomic 5A (9) has the homozygous speltoid phenotype. The nullisomics for the 21 chromosomes have been identified and studied in the progeny of the corresponding monosomics in the Chinese variety. All of them are less vigorous, some more so than others. About half are either ♂ or female sterile. Nullisomic 4D (15) has pollen that appears normal, but is incapable of inducing fertilization (Sears 1954). Seven are male sterile but have some fertility on the female side; three are female sterile, the others show at least some male and ♀ fertility. Only one, number 7B (7), is carried on regularly as a nullisomic stock. The phenotypic differences between the different nullisomics are useful in determining which chromosome is missing, but they are likely to differ in different varietal backgrounds.

When grown in the field, natural crossing in nullisomic plants is very frequent. It occurs also in normal varieties as well as in the monosomics. For careful genetic studies it is necessary to bag the heads and control such insects as thrips.

CYTOLOGICAL BEHAVIOR. The univalent chromosome in a monosomic plant shows at meiosis the typical behavior expected of an unpaired chromosome, frequent failure to arrive on the metaphase I plate, lagging, or occasional division at metaphase I probably followed by lagging at division II.

The relatively high frequency of asynapsis in nullisomic 3B and the consequent lagging of other chromosomes, also the gene for asynapsis have been mentioned. One nullisomic has been found to have the opposite effect (Riley 1958, Riley and Chapman 1958, Sears and Okamoto 1958). Riley reported that the absence of a particular chromosome in haploids (nulli-haploids) greatly increased the frequency of bivalents and trivalents. As many as 19 of the 20 chromosomes were observed in various associations whereas in 21-chromosome haploids, the maximum number was 9. In nullisomics with this same chromosome missing (20 II), multivalent associations of 3, 4, 5 and 6 chromosomes were common. More than half the cells had at least one multivalent and many had several. In 21 II derivatives and in the monosomic, pairing was normal. Pairing was likewise normal in a 2n + telocentric for the long arm of this chromosome (long arm more than twice the length of the other). Hence the gene for prevention of pairing of homoeologues must be in the long arm. Sears and Okamoto (1958) reported that when chromosome 5B (5) was missing there were many more bivalents in hybrids between hexaploid wheat (AA BB DD) and the amphidiploid, AADD, from T. aegilopoides x Aegilops squarrosa and also in hybrids of AABBDD with AA. It is probable that this is the chromosome missing in Riley's material described above. The conclusion is that the long arm of chromosome 5B (5) has acquired a mutation that limits pairing to chromosomes that are strictly homologous, thus furnishing the means by which tetraploid and hexaploid wheats may have achieved diploid pairing. This gene is not likely to be present in the diploid species that are the probable parents of the allopolyploid T. durum and T. vulgare wheats. This probably accounts for the reports that amphidiploid hybrids from crosses between the diploid species show higher frequencies of multivalents than do the natural allopolyploids, as pointed out by Riley et al. (1958).

The evidence is against the origin of the tetraploid wheats from autotetraploids, but the results furnish evidence of a possible mechanism by which an autotetraploid or crosses between closely related species could achieve diploid pairing. This knowledge opens up numerous applications for research and for practical breeding. It is one of the important advances that has been made in cytogenetics.

BREEDING BEHAVIOR (TRANSMISSION). Information on the frequency of monosomics in the progeny of monosomics used as the ♀, as the ♂ in crosses with normal, and in selfs has been reported by Sears (1944, 1952, 1954). Based on the progeny of monosomic 5A (9) pollinated by normal pollen, the following female gametes functioned to produce 785 plants that survived to maturity:

Female Gametes		Constitution of offspring	%
628 with no 5A	=	20 II + I	80.0 monosomic
129 with a normal 5A	=	20 II + II	16.4 disomic
16 with a telocentric 5A	=	20 II + I + telo.	3.6
11 with an iso-5A	=	20 II + I + iso.	
1 with a normal 5A + telocentric	=	21 II + telo.	

As shown in the above tabulation, in addition to monosomics and normals, there were about 3.6% of other types with a telocentric or an isochromosome. These will be discussed later. In the above test, about 80% of the progeny were monosomic. An average value of 75% for all the monosomics is a close approximation. The range for different monosomics is far less than for Nicotiana tabacum (page 227).

Functioning of the 20-chromosome ♂ gametes was 8%, based on 106 offspring from three different monosomics crossed on normals. The pollen in each of the monosomics was normal in appearance (Sears, personal communication). The low frequency of monosomics through the male was therefore the result of the inability of n-1 pollen to compete with n pollen. The frequency of nullisomics among the self progeny of monosomics was 3.98% based on 19,114 plants from self-pollinated monosomics, with a range from about 1 to 8%.

Based on assumed values of 75% n-1 for ♀ gametes and 8% of functional n-1 ♂ gametes, the expectations from selfing a monosomic are those given in Table 111 in the form of a checkerboard square:

Table 111. Expected frequencies of the different chromosome types in the F_2 progeny of a monosomic with assumed (n-1) transmission rates of 75% through the ♀ and 8% through the ♂.

	through ♂	
through ♀	n = 92%	(n-1) = 8%
n = 25%	2n = 23%	2n-1 = 2%
(n-1) = 75%	2n-1 = 69%	2n-2 = 6%

As shown in Table 111, the expected ratio of 2n:2n-1: 2n-2 i.e. disomics: monosomics: nullisomics is 23:71:6, and the ratio of disomics: monosomics is about 1:3.

Most of the time the monosomics in the progeny are monosomic for the same chromosome that was deficient in the parent. Occasionally, however, monosomics for other chromosomes may occur also in the progeny, a phenomenon that has been termed "univalent shift", by Person, (1956). It should be relatively frequent in the progeny of nullisomic 3B; and it probably occurs more frequently in the progeny of crosses with certain varieties than with others (Burnham, unpublished). This is no different, in principle, from the fact mentioned earlier that trisomics in diploids show a higher frequency of non-disjunction for other chromosomes than is observed in their diploid sibs. In Drosophila a higher rate of non-disjunction for the X chromosome in Triplo-4 flies has been observed (Sandler and Novitski 1956). Their conclusion that it furnishes evidence of homology between X and 4 does not seem justified. If a similar line of reasoning is followed, the higher rates of non-disjunction for chromosomes other than the trisome in Datura and chromosomes other than the monosome in T. vulgare should be considered evidence of additional homologies. A more likely explanation is a general physiological effect on pairing.

The cross between a nullisomic and a normal plant is expected to produce only monosomic progeny. However, a cross of Redman wheat nullisomic 7D (21) x Prelude produced 8 plants only one of which was monosomic (McGinnis and Campbell 1958, 1960). Five of the others were triple monosomics (18 II + I + I + I), and two were double monosomics (19 II + I + I). There was sufficient ovule fertility (0 to 39%, avg. 38% for the double monosomics, 0 - 39%, avg. 23% for the triple monosomics) to maintain the deficient stocks.

Certain precautions must be taken in studies using the monosomics. Accurate chromosome counts should be made of the number of pairs and univalents. Shift to a different monosomic must be guarded against. The morphology of the univalent chromosome should be noted, since for certain chromosomes relative arm length and total length are distinctive. For some work the 20 II + telo. or 20 II + iso. stocks (mono-telo or mono-iso) or di-telos can be used to check if the univalent chromosome in the monosomic is the normal homologue expected. Also the different nullisomics have distinctive growth characteristics which can be used, but comparisons must be made in material with the same varietal background. A final check can be made by crossing the monosomics with the two tetrasomics that have a specific compensating effect for that monosome (see below). For certain ones, easily classified genetic markers are available for use in checking particular chromosomes. Eventually, they may become available for other chromosomes.

Telocentric and iso chromosomes in wheat

The univalent chromosome in monosomics misdivides at the centromere at times giving rise to telocentric or to isochromosomes. As shown earlier, page 231, in the progeny from monosomic 5A(9) crossed with normal about 3.6% had either a telocentric or an isochromosome. Sears concluded that misdivision of the univalent occurs at division I or II of meiosis. Misdivision for any of the chromosomes may occur also in somatic divisions, resulting in sectorial chimeras (Sears 1954). Monotelosomic or monoisosomic stocks have been established for each of the 21 chromosomes, but in most cases only one of the two possible types (Sears 1946). Many of them show increased vigor and fertility over the corresponding nullisomic, to the extent that they can be maintained as stocks and used in crosses.

For 20 of the lines in Chinese, stocks with either 20 II + iso, or 20 II + telo are being used by Snyder, et al. (1958) in the production of chromosome substitution lines (see page 246). For chromosome 20, a monosomic line is being used. When they are

crossed with a normal variety, the progeny include monosomic plants (20II + I) and plants that are 20 II + telo + the normal homologue; or 20 II + iso + normal, and in addition the derived types from the isochromosome or the telocentric chromosome. In general, the transmission frequency through the female of mono-isochromosomes or mono-telocentrics is similar to that for monosomics. Transmission frequency through the male is not the same. In general, microspores carrying a telocentric (20 + telo) have less advantage over the n-1 spores than do n over n-1 spores. However, in plants mono-telosomic for the long arm of 5A (9), the 20 + telo spores have about the same advantage as n over n-1. Microspores with an iso-chromosome (20 + iso) have still less advantage over spores with n-1 chromosomes. For a mono-isosomic for the long arm of 5A (9), Sears (1952) reported that the functioning male gametes included 26.4% nulli, 30% derived telocentric, and 43.6% mono-iso.

The breeding behaviors of six mono-telosomics and mono-isosomic stocks when self-pollinated to maintain them are shown in Table 112.

Table 112. Summary of types of progeny from selfs of plants mono-isosomic or mono-telosomic for chromosomes 1D (17), 4A (4), 5A (9), 6A (6), 6B (10), and 6D (19) (Sears, 1954, from Table 11, p. 36, Missouri Research Bulletin 572). The telo- and the iso- for the same chromosome involve the same arm.

Chromosome	Total no. plants	Number analyzed	% * nulli	No. of Plants mono-telo-	mono-iso-	di-telo-	di-iso-	telo-+iso-
1 D (17) iso-	45	12	13.3	0	5	0	1	0
4 A (4) "	92	47	31.6**	3	14	0	0	1
5 A (9) "	276	161	13.8**	25	68	0	21	9
6 A (6) "	51	15	13.7**	1	7	0	0	0
6 B (10) "	155 R	72	3.9	0	40	0	25	1
6 D (19) "	37	5	8.1	0	2	0	0	0
Total, Avg. %	656	312	14.1					
1 D (17) telo-	168	65	1.2	45	2	16	0	0
4 A (4)	24	14	8.3**	9	0	3	0	0
5 A (9)	450	376	3.1**	354	---***	---***	0	8
6 A (6)	127	46	3.9**	32	0	9	0	0
6 B (10)	21 R	12	0.5	5	1	4	0	0
6 D (19)	85	43	3.5	31	0	9	0	0
Total, Avg. %	875	556	4.9					

* based on total number of seedlings.

** nullisomic not distinguishable with certainty from mono-telosomic or mono-isosomic as seedlings.

*** scored genetically, could not distinguish di-telo from mono-isosomic.

The data in Table 112 show there is a much lower frequency of the mono-iso or mono-telo parental types among their self progeny than there is of monosomics among the self progeny of monosomics; the frequency for the mono-isosomic being much less than for the mono-telosomic (16.0 vs. 38.1%).

Nullisomic offspring were more frequent among the progeny of 20 II + iso plants than among the progeny of 20 II + telo plants for five of the six chromosomes shown in Table 112.

The differences in percentages of nullisomics are in part a result of differences in ability of n-1 pollen to compete with n, as mentioned earlier. The progeny of the selfs of mono-telo's and mono-iso's also include di-types from the functioning of 20 + telo or 20 + iso pollen, and derivative types, i.e. telocentrics from isochromosomes and isochromosomes from telocentrics. Stocks might be maintained as di-telos for use in verifying monosomic transfers. In the production of substitution lines, mono-telocentric plants are used. These could be selected among the progeny of crosses between monosomic and di-telosomic plants.

Speltoids and fatuoids and related behavior in wheat and oats

Speltoids and fatuoids

In cultivated bread wheats (2n=42), mutants appear that have a complex of linked characters resembling Triticum spelta, and in cultivated oats, Avena sativa (2n=42), mutants that resemble Avena fatua, wild oats, a noxious weed. On mature heads of speltoid wheat plants, the outer or empty glumes are short, almost square across the top, strongly keeled and highly indurated. The spikes are long and slender with the spikelet nodes far apart. The rachis is not brittle as it is in T. spelta. The heterozygous plants are usually taller than normals. The grains on fatuoid plants in oats are shed as soon as ripe due to their having an oval disarticulation surface or "sucker mouth", whereas in normal oats disarticulation is by fracture. Other characters are a dense pubescence at the base of the grain and a twisted awn on each grain of the spikelet. Normally there is little or no pubescence and a weak awn or none on only the larger grain. The breeding behavior of these and related off-types has been the subject of extensive investigations. A review by Huskins (1946) summarized the results to that date. The brief survey here attempts to relate the results to those with the monosomics and other aneuploids. Monosomics and related aneuploid types in Avena sativa have not been discussed up to this point, but they do occur.

Speltoids and fatuoids occur first as heterozygotes and have originated under conditions where there was no opportunity for natural crossing with T. spelta or A. fatua. They are similar to the variety they came from except for this complex of characters. The "mutation" theory of their origin is favored by the fact that oat plants have been found with sectors or mosaics of fatuoid-type and normal grains. In cultivated oats growing where A. fatua is present as a common weed (as in Western Canada), natural crossing is a problem since it does occur and is another source of off-types.

Work on speltoids was begun by Nilsson-Ehle in 1904. Later he reported that heterozygotes when crossed with normal ♂ or when selfed gave 1 Normal:1 heterozygote but that the reciprocal cross of normal x heterozygote (♂) gave all normal offspring. In 1920 he reported there were roughly three ratio-types of normal: heterozygote: homozygote, i.e., 1:2:1; 1:5:0+, and 1:1:0+, first labeled the A-, B-, and C- series but later designated α, β, γ. The three series are about equally frequent. Various variants of these ratios have been reported. Many explanations were offered, but none was successful until a scheme was devised based on cytological information. Winge, the first to recognize the importance of hybridization followed by chromosome doubling in speciation, reported occasional figures with 19 II + IV in speltoids; in other types 41 chromosomes, or other irregular behavior (Winge 1924). A 3-1 segregation from the quadrivalent could furnish the n-1 spore for the 41 chromosome type. Through concepts developed by Nilsson-Ehle and his group and Winge, it was postulated that different genomes had factors which tended toward different types of wheat, and that occasional pairing between chromosomes of different genomes could result in plants with different dosage of certain of these chromosomes. This pointed the way for cytological analysis. The early workers used