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

the paraffin method, later ones the smear technique. After 1929 when McClintock discovered that heat applied to the smears greatly improved the spreading and destained the cytoplasm, Huskins stated that his group had rechecked all their earlier cytological observations.

The speltoid "mutation" involves two gene complexes, one affecting glume characters, the other awn characters; these being 30-40 units apart on chromosome 5A (9). In most "mutations", both go together, indicating a chromosome rather than a single gene mutation. Different dosages of these genes produce markedly different phenotypes.

The β series of heterozygous speltoids in wheat or heterozygous fatuoids in oats have 41 chromosomes, and are monosomic for a particular chromosome. In wheat this chromosome is number 9 which carries a speltoid suppressor. Plants nullisomic for 9 have the homozygous speltoid phenotype since the suppressor is absent. Plants monosomic for 9 (hemizygous), show partial suppression of the characters and have the heterozygous speltoid phenotype. The ratio from the cross of monosomic 9 x normal ♂ is about 1:3 or 1:4 of normals to heterozygotes (monosomics). Normal x heterozygote gives mostly normals, since the 20-chromosome spores rarely function in the pollen. A modified β series has a high frequency of functioning 20-chromosome microspores and the F_2 progeny include 40-chromosome sterile dwarfs. There is no explanation for the difference in frequency of functioning, but the n-1 pollen must be at less of a disadvantage against the other class of pollen (with a modified 9) than against normal pollen.

Other aberrants have chromosome 9 present only as a telocentric, or as an isochromosome. Still others have a small or a large deficiency for a portion of 9 (less than one arm missing). Those belonging to the γ series have a large deficiency, but the α series lines which give 1:2:1 or 1:1:0 may have no detectable deficiency. Other off-types are trisomics that resemble T. compactum, and are termed compactoids.

Similar series are found in oats, but there is in addition a larger variety of off-types. The fatuoid complex shows no crossing over between the characters. Some off-types have certain characters resembling A. sterilis, the Mediterranean wild oat, e.g. those called steriloids and subfatuoids have florets that remain together on threshing. In oats, heterozygous fatuoids are not taller and are less distinctive. The off-types recognized are more likely to be homozygous fatuoids in the β and γ series but they are usually sterile. Those belonging to the α series are therefore the ones usually studied, also they could accumulate since they are not easily recognizable.

Monosomics in oats have been studied also by Costa-Rodrigues (1954). Their production was facilitated by the use of X-rays. The percentage of nullisomics among the progeny of five monosomics varied from 2.1 to 46.0%. Similar results were reported by O'Mara (1961). A late-generation line from a cross between two varieties was found to be segregating albino plants which had 40 chromosomes (McGinnis and Taylor 1961). Their sibs with 42 and 41 chromosomes were green. The percentage of nullisomic (albino) plants was 63.9.

Somatic segregation

A certain 42-chromosome stock of Avena sativa has been reported to segregate normal and 40-chromosome dwarf plants in a ratio of about 9:1 (Griffiths and Thomas 1953). All the normal plants showed this segregation in their progeny. Outcross seed produced only normal plants, part of which again segregated dwarfs. Meiosis was normal in the plants whose progeny segregated, but root tips from the germinating seeds showed that those which developed into sterile dwarfs already had only 40 chromosomes. Apparently, a certain recessive genotype brings about the loss of a particular pair of chromo-

somes between fertilization and maturation of the embryo. It was suggested that the last mitotic divisions in that process may be especially prone to non-disjunctional behavior.

Aneuploids in the Emmer wheats

Monosomics have not as yet been established for the Emmer wheats. One easily tested source of such monosomics should be interchange heterozygotes, since they regularly produce at meiosis a low frequency of n-1 spores by 3-1 disjunction in the ⊙4. Compensating tetrasomic-monosomic lines or trisomic-monosomic in a 14 II wheat were being established by the late J. Longwell in Sears' laboratory.

Addition and substitution lines (also see p. 259)

Matsumura (1953) reported types that he termed D-haplosomic in which one D chromosome had been added to the diploid (14 II) Emmer set. The characters by which a particular 29-chromosome line differed from the Emmer parent served to locate certain genes carried by that D chromosome. Plants with 28, 29 and 30 chromosomes appeared in their progeny. Lines having an added pair of chromosomes from another species have been produced for vulgare wheat also: rye added to wheat, first by O'Mara (1940 and 1951); and Aegilops umbellulata to wheat by Sears (1956). Head and plant characters were markedly different.

O'Mara produced lines of T. vulgare wheat also in which a pair of rye chromosomes (the one carrying hairy neck) was substituted for a pair of wheat chromosomes. This had a lesser effect on the phenotype than did the addition of the same pair to the full set of wheat chromosomes.

Trisomics and tetrasomics in wheat

Trisomic plants were found among the progeny of haploids and triploids of T. vulgare. Sears has established the complete set of 21 in Chinese. Most are nearly normal in appearance, except 5A (9) which has the compactoid phenotype and 2B (2), 2A (13) and 2D (20) which are narrow leaved. The breeding behaviors of trisomic and tetrasomic plants whose progeny were completely analyzed cytologically are summarized in Table 113 (Sears, 1954).

Table 113. Summaries of completely analyzed progeny of trisomic and of partially analyzed tetrasomic plants selfed (Sears, 1954, from Tables 7 and 8, Missouri Research Bulletin 572).

Parental type	Total No.	Types and observed nos.				number in %			
		2n + 1	2n + 2	2n	Others	2n + 1	2n + 2	2n	Others
2n + 1	279	125	3	151		45*	1 +	54.1	
2n + 2	462	109	341	9	3	23.6	73.8**	1.9	0.6***

* ranged from 35 to 52%

** ranged from 45 to 100%

*** 1 iso, 1 telo, 1 haploid

As shown in Table 113, tetrasomics do occur in the self progeny of a trisomic, but with a low frequency. A complete set of 21 tetrasomic lines has been established in Chinese. Disjunctions of 3-1 type in the tetrasome must have occurred also as shown by the occurrence of 2n and 2n + 1 plants in the progeny. Pollen with the n number was

probably favored over that with n + 1 in the trisomics.

Vigor and fertility of the tetrasomics are below normal, but less so than for the corresponding nullisomics. The tend to differ from normal in a direction opposite to the nullisomics. All tetrasomics are both female and male fertile.

Identification of chromosomes belonging to the different genomes

Crosses of the different monosomics with T. durum have served to identify those belonging to Emmer, i.e. the A and B genomes. The method of determining which monosomics belonged to the durum group and which to the D genome was similar to that used in Nicotiana, i.e. cross the 2n -1 plants, of T. vulgare with the 14 II species, e.g. T. dicoccum. Counts of the number of pairs and univalents in the monosomic F_1 plants were used to determine if the univalent in the monosomic T. vulgare parent belonged to the D or the AB genomes (see page 227). Those for the AB genomes were arbitrarily assigned numbers 1 to 14, those for the D genomes 15 to 21. Monosomics for the D genome were established and identified also by Matsumura (1952, 1952a, 1953).

To distinguish the chromosomes belonging to the A genome from those belonging to the B genome, a different technique was used by Sears (1956a), and Okamoto (1957, 1962). Plants having 20 II + telo for chromosomes in the A and B genomes were crossed with the amphidiploid (AADD) of T. aegilopoides x Aegilops squarrosa. In the F_1's, if the telocentric were from an A chromosome, it would be expected to pair with an A chromosome from the ♂ parent and form an unequal bivalent. If the telo were from a B chromosome, it should have no normal mate. Hence, crosses showing high frequencies of unequal bivalents indicated the unequal pair belonged to the A genome; those with few or no heteromorphic bivalents indicated that the telocentric belonged to the B genome. Using these tests, they succeeded in identifying the chromosomes belonging to the A and B genomes, as shown by the numbers in parentheses in Table 114.

Table 114. Chromosomes belonging to the A, B and D genomes in T. vulgare. The numbers in parentheses are the original numbers assigned to these chromosomes. The chromosomes are now numbered to indicate the homoeologous group as well as the genome to which each belongs, e.g. 1A, 1B and 1D belong to the first group: (Okamoto, 1962, Table 3, p. 36, Vol. 4, Canadian Journal of Genetics and Cytology).

Genome A		Genome B		Genome D	
1A	(14)	1B	(1)	1D	(17)
2A	(13)	2B	(2)	2D	(20)
3A	(12)	3B	(3)	3D	(16)
4A	(4)	4B	(8)	4D	(15)
5A	(9)	5B	(5)	5D	(18)
6A	(6)	6B	(10)	6D	(19)
7A	(11)	7B	(7)	7D	(21)

* small satellite

The identification is being checked further by Snyder (unpublished) by means of interchanges that mark the chromosomes of the A genome. A group of marker interchanges in T. monococcum established by Yamashita (1953) has been transferred to T. durum by repeated backcrosses to T. durum. These were then crossed with the monosomics for chromosomes 1 to 14 in T. vulgare. Cytological examination of the monosomic F_1's has shown a chain of 3 in certain crosses, and a ring of four and a univalent in others. The chain of three must indicate that the missing chromosome is one that is involved in the interchange used to mark two of the A chromosomes.

Identification of homoeologous sets of chromosomes

As already mentioned, the presence of an extra chromosome may compensate phenotypically for the absence of a particular chromosome. For example, plants nullisomic for chromosome 20 in Chinese were described as: somewhat dwarfed, leaves short and slightly narrower than normal, male fertile, but female sterile. Plants nullisomic for this chromosome but also tetrasomic for chromosome 2 were nearly normal and fertile as shown in Fig. 54. The same was true for plants nullisomic for 20 but tetrasomic for 13. That is, two extra doses of the genes in chromosome 2 or 13 were able nearly to compensate for the absence of the genes in chromosome 20. Further tests indicated that for these three chromosomes, the nullisomic for any one could be compensated for by an extra pair of either of the other two. None of the other chromosomes tested was able to accomplish this for nullisomic 20. This was interpreted as evidence of partial homology (homoeology) between these three chromosomes; each of which belongs to a different genome. The tests for compensation have been extended to the point where the 21 T. vulgare chromosomes can be placed in seven groups of three each; the characteristic of each group being that the nullisomic for any one of the three can be compensated for by extra doses of either of the other two, (Sears 1954, Sears and Okamoto 1957). The tests not showing compensation "have fallen into three classes: 1. The monosomic-tetrasomic is sterile * *, 2. The monosomic-tetrasomic is more or less fertile * * * but is inferior to both the monosomic and the tetrasomic and 3. The nullisomic-tetrasomic is inferior to the nullisomic concerned. Many are extremely abnormal" (Sears, personal communication). These relationships agree with the other evidence that hexaploid wheats have three different genomes.

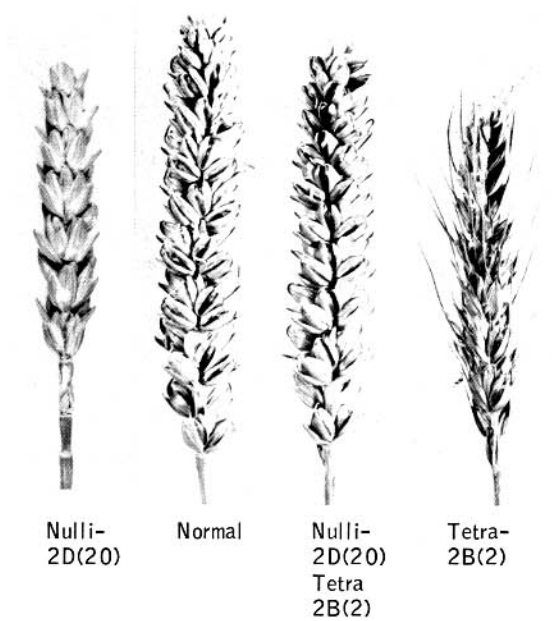

FIG. 54. Spikes showing ability of tetrasome 2B (2) to compensate for nullisome 2D (20) (from Sears, 1944, Fig. 2, p. 232, Genetics 29).

The chromosomes are now numbered to indicate the homoeologous group as well as the genome to which they belong (Table 114). For example, the first homoeologous group is 1A, 1B and 1D. The earlier numbers for each are in parentheses.

Trisomics are able to bring about partial compensation within a homoeologous

group. This ability accounts for the occurrence of specific trisomics among the self progeny of a particular nullisomic that sets seed, exclusive of nullisomic 3B (3) which has a high frequency of asynapsis. Also in a nullisomic plant, microspores with an extra chromosome are favored when that chromosome compensates at least in part for the missing one.

The pairs with satellites and secondary constrictions were identified as chromosomes 1 and 10 (Morrison 1953). Chromosome 1 is the longer of the two, is the more heterobrachial, and has the smaller satellite. Reference to the above list shows they belong to the B genome. Since T. monococcum with the A genome has two pairs with satellites (Burnham, unpublished), the satellites must be suppressed in hexaploid wheat or they have been lost.

Certain varieties of T. vulgare wheat differ from the Chinese variety by one or more interchanges. The Thatcher variety has an interchange between chromosomes 4 and 10. New interchanges have appeared also in the 2n progeny from haploid Triticum vulgare (Sears and Okamoto 1958). These would be expected if exchange occurs between the chromosomes that occasionally pair in the haploid. The chromosomes of 13 of those interchanges have been identified. Nine of them were between homoeologs, four were not. These results indicate that association and exchange are not at random, but are more likely to involve homoeologs, although not exclusively so.

Special methods of locating genes

The number of useful qualitative genetic characters in wheat is limited. There is only one chlorophyll mutant (Neatby's virescent), no good endosperm characters, probably three factors for seed color; several head characters including hooded, awnless, dense (compactoid), glume shape (speltoid); and several plant characters, coleoptile and stem color, pubescent node, glossy sheath, and liguleless. In addition there are the factors for disease resistance, e.g. for stem and leaf rust, mildew, and bunt. The F_2 ratios for certain of these characters in normal hexaploid wheat are 3:1; for others, including many of the leaf and stem rust reactions to individual races, there are also other types of interactions of two factor pairs resulting in 9:7, 15:1 or 13:3 ratios with resistance dominant in certain cases, recessive in others (Hayes et al.). Resistance to the large number of races of rust may be governed by many genes. For example, in a study of leaf rust resistance, not using monosomics, Martinez et al. (1953) found evidence of six different genes, each segregating 3:1 for reaction to a particular race, but closely linked, the total distance being about six units. The reaction to other races in this same study appeared to be governed by two or more factors. In certain varieties the reaction to a single race of stem rust may be governed by several factors (Plessers 1954, Pi 1961).

With such a limited number of genetic markers, practically no progress had been made in establishing linkage groups. The monosomics have made it possible to accomplish this in wheat.

A list of the characters and the chromosomes on which major genes are located is in Table 115.

Factors have been located in 20 of the 21 chromosomes. Factors for stem rust resistance effective from the seedling stage on to later stages have been found in 11 chromosomes. In general, the methods used in locating these factors and the expected ratios are similar to those described for Nicotiana tabacum (page 228). In wheat there seems to be a more uniform rate of transmission; also nullisomic offspring are usually obtained in the self progeny of a monosomic.