CYTOGENETIC STUDIES WITH POLYPLOID SPECIES OF WHEAT. II. ADDITIONAL CHROMOSOMAL ABERRATIONS IN TRITICUM VULGARE[1]

E. R. SEARS

U. S. Department of Agriculture, Columbia, Missouri

Received October 22, 1943

INTRODUCTION

MONOSOMES are very useful in the genetic analysis of a species, as CLAUSEN (1941a) has pointed out, since they greatly facilitate the locating of genes on the chromosomes. The loss of an entire chromosome from a strictly diploid organism, however, is too deleterious to be tolerated; and thus the method of monosomic analysis is possible only in polyploid organisms, where the added chromosomes tend to counteract the effects of chromosome losses.

Of still greater value for genetic analysis where they can be obtained are nullisomes, which are deficiencies for both members of a pair of chromosomes. Only in the higher polyploids, however, such as the allohexaploid *Triticum vulgare* (n = 21), common wheat, are nullisomics viable.

During the past several years, numerous nullisomes, tetrasomes, and other aberrations have been accumulated in *T. vulgare*. An account of the origin of part of this material was given in the previous paper of this series (SEARS 1939), and a brief description of seven nullisomics was published in 1941. The present report aims to bring the account up to date. More detailed presentation of some of the data will be made in subsequent papers.

MATERIALS AND METHODS

All of the aberrations have occurred in the wheat variety Chinese Spring. As described in a previous publication (SEARS 1939), 16 monosomes and five trisomes were found in the 11 aberrant offspring of a monoploid pollinated by a diploid. Through selfing of plants possessing these aberrations, the corresponding nullisomes and tetrasomes have been obtained. One of these nullisomes, which renders plants partially asynaptic without unduly depressing their fertility, has provided a ready source of additional monosomes and trisomes. A few monosomes and nullisomes were kindly supplied by DR. J. G. O'MARA, from certain of his cultures of wheat-rye derivatives.

Part-chromosome aberrations, consisting of telocentric chromosomes and isochromosomes, have occurred frequently. They have appeared mainly in offspring of monosomic plants, presumably following misdivision of univalents.

[1] These studies are part of a program supported by funds obtained under Bankhead-Jones Project SRF 2–5, "Comparative Genetics and Cytology of Polyploid Series in Triticum." Cooperative investigations between (1) the Division of Cereal Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. DEPARTMENT OF AGRICULTURE, and (2) the Field Crops Department, MISSOURI AGRICULTURAL EXPERIMENT STATION. Journal Paper No. 921 of the Missouri Station.

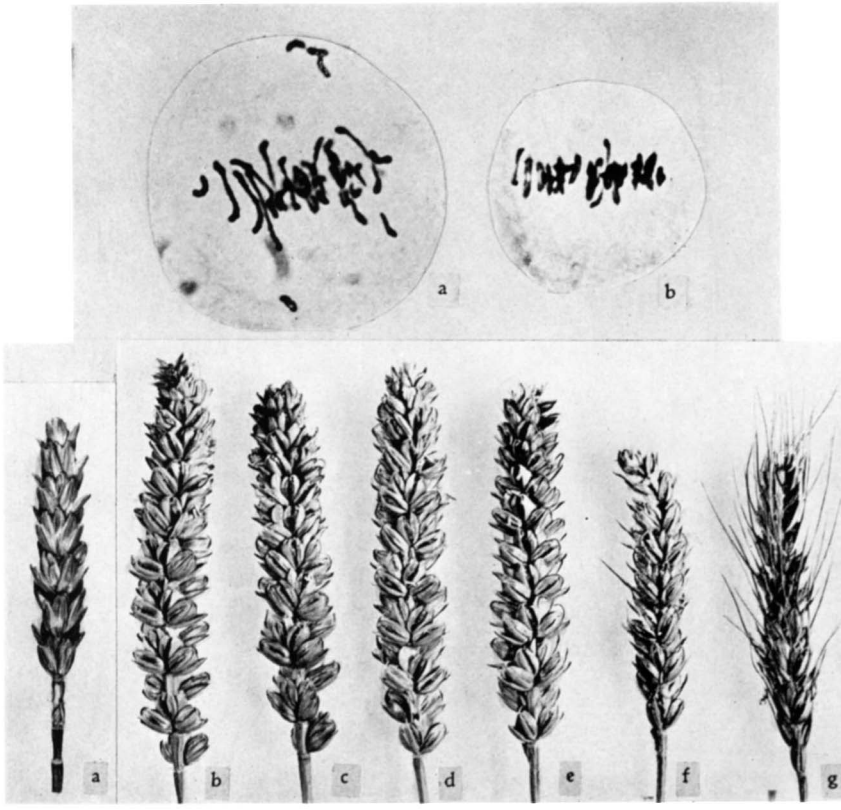

FIG. 1 (above). MI in microsporocytes from (a) nullisomic-III and (b) normal plants. The former cell shows a reduced frequency of chiasmata and six univalent chromosomes. ×547 and 456, respectively.

FIG. 2 (below). Spikes showing ability of tetrasome II to compensate for nullisome XX. (a) Nulli-XX, (b) mono-XX, (c) mono-XX, tri-II, (d) normal, (e) nulli-XX, tetra-II, (f) tri-II, (g) tetra-II. All ×0.625

Cytological observations were made from microsporocytes smeared in aceto-carmine after fixation of whole spikes for about two days in Carnoy's solution. Simple determinations, such as the number of monosomes present, were frequently made with a high-dry objective from preparations with no cover slip. Most other observations were from freshly prepared slides, although some were from permanent preparations. Most of these permanent slides were made by the tertiary-butyl-alcohol method outlined in a previous publication (SEARS 1944).

MONOSOMES AND NULLISOMES

Review of literature

Although monosomes have been observed fairly frequently in polyploid species, nullisomic plants have seldom been reported. CLAUSEN (1941a) has isolated at least 20 of the 24 possible monosomic types in *Nicotiana Tabacum*, but thus far he (1941b) has obtained no nullisomics. In hexaploid *Avena sativa*, HUSKINS (1927) found that certain homozygous fatuoids (resembling *A. fatua*) have only 20 pairs of chromosomes, and PHILP (1935, 1938) isolated two additional nullisomics.

In the hexaploid wheats (Triticum) nullisomics have been reported by a number of investigators, but many of these deficiencies have evidently involved the same chromosome, the "C" or speltoid chromosome. Speltoidy (so called because of the resemblance to *T. spelta*) has been shown by WINGE (1924), HUSKINS (1928), PHILIPTSCHENKO (1929), HÅKANSSON (1930), BYNOV (1938a), and MATSUMURA (1939) frequently to be due to the effects of a particular monosome or its corresponding nullisome. Nullisomic dwarfs or semi-dwarfs have been reported by KIHARA (1924) among derivatives of *T. polonicum*×*T. spelta*, by THOMPSON (1928) following a varietal cross in *T. vulgare*, and by UCHIKAWA (1938). LOVE (1940) found several nullisomic plants and even nullisomic lines in 50 strains (F_5 to F_7) selected for agronomic characters from hybrids of *T. vulgare*×*T. durum;* most of these nullisomics were to some extent fertile.

Several dwarfs in wheat have been observed which were not thoroughly investigated cytologically, if at all, and some of these may have been nullisomic types. Such dwarfs were reported by FARRER (1898), RICHARDSON (1913), NEETHLING (1917), CUTLER (1919), THOMPSON (1922), and WALDRON (1924), mostly following varietal hybridization. The occurrence of normal plants among the offspring of certain of these dwarfs may be explained as the result of natural cross-pollination of nullisomics by normal plants. Nullisomics, which are frequently of reduced male fertility, are particularly subject to such crossing. The crossed seeds would have yielded monosomic plants, which would probably have been reasonably normal in appearance. The absence of dwarfs in the progeny of these normal-appearing plants could have been due to too small populations, since nullisomics are rather rare in the progeny of certain monosomics.

Chiefly because the nullisomics which have been reported in hexaploid wheats have occurred for the most part in different varieties, or even in

derivatives from hybrids with tetraploid species, it is impossible to conclude how many different chromosomes have been concerned. It seems probable, however, that the number is comparatively low. Most of the deficiencies (except those reported by LOVE) have been discovered first in monosomic condition, through morphological peculiarities of the monosomic plants; and the present investigation indicates that there are few monosomics in *T. vulgare* which differ appreciably from normal.

Description of nullisomic plants

Seventeen of the possible 21 different nullisomes in *Triticum vulgare* have now been obtained. These have been designated I to XI and XV to XX, respectively, according to whether or not the missing chromosome is homologous to any of the 14 chromosomes in the haploid complement of *T. durum*. Within these two groups the chromosomes have been numbered according to the order in which the nullisomic types were found. Nullisomics I to V, XV, and XVI have already been briefly described (SEARS 1941).

Only the most striking characteristics of the nullisomic plants will be noted here, since a complete description is contemplated when as many as possible of the remaining four nullisomics have been obtained.

Nullisomic I. Spikes less dense than normal. Glumes darker-colored and somewhat stiffer. Fertility 50 percent or more in some early spikes but usually zero in later spikes.

Nullisomic II. Tillering much reduced. Maturity delayed. Culms short and thick. Leaves broad. Spikes short and thick, frequently with one or more reduplicated spikelets. Female sterile. Completely awnless, whereas normal plants have "hooded" (reduced and recurved) tip awns.

Nullisomic III. Culms short. Leaves narrow. Spikes short and compact. Two or more univalents usually present at meiotic metaphase. Fertility fair, with seed set reaching 100 percent in some artificially pollinated spikes.

Nullisomic IV. Narrow culms and leaves. Spikes nearly normal in appearance, but usually male sterile.

Nullisomic V. Culms short and thin. Leaves narrow. Spikes small, with small glumes and indehiscent anthers. Maturity delayed.

Nullisomic VI. Culms short and thin. Leaves narrow. Spikes short and of straggly appearance due to narrow, spreading outer glumes. Fertility low.

Nullisomic VII. Most nearly normal of the 17 nullisomics. Culms slightly shortened, and fertility reduced in upper portion of spike.

Nullisomic VIII. Strongly increased tillering. Culms much reduced in length and diameter. Leaves narrow. Spikes small, with awns straight and somewhat longer than normal. Maturity delayed. Male sterile.

Nullisomic IX. Homozygous speltoid. Culms and leaves narrow. Nonpubescent nodes. Maturity delayed. Spikes lax, narrow. Glumes small and stiff. Awns somewhat increased in length. Male sterile.

Nullisomic X. Culms short and thin. Leaves narrow. Maturity delayed. Spikes short. Outer glumes slender and spreading. Awns distinctly longer than normal. Male sterile.

Nullisomic XI. Fertility reduced. Two or more ovaries (up to four) in occasional florets.

Nullisomic XV. Thin culms and narrow leaves. Spikes short and usually dense. Male sterile, although anthers dehisce.

Nullisomic XVI. Culms short. Leaves narrow. Spikes short, very dense, and frequently bent or curled. Maturity delayed. Fertility very low. Seeds white instead of the normal light red.

Nullisomic XVII. Culms short and thin. Spikes lax and tending to be shortened by abortion of terminal spikelets. Fertility strongly reduced.

Nullisomic XVIII. Extremely fine-leaved and weak in seedling stages, but reasonably vigorous at maturity. Very late. Spikes small and slender. Reduced female fertility. Apparently male sterile, although anthers dehisce.

Nullisomic XIX. Long, lax spikes with a straggly appearance due to outer glumes being narrow and spreading. Fertility reduced.

Nullisomic XX (fig. 2a). Very similar to nulli-II, except slightly more vigorous, less coarse, and slightly female fertile.

To summarize the data on fertility of the 17 nullisomics, none is completely sterile, ten or 11 are fertile to some extent as both male and female, five or six are fertile on the female side only, and one is fertile on the male side only.

The nullisomics show the location of several of the known genes in wheat. A gene for red seeds is shown to be located on chromosome XVI—that is, on the chromosome which is absent in nullisomic XVI. The factors for pubescent nodes, squareheadedness and suppression of speltoidy, already known to be linked together on the speltoid chromosome, prove to be located on the chromosome here designated IX. Data are also supplied concerning the genes affecting awn development. WATKINS and ELLERTON (1940) find Chinese wheat to have the genetic constitution *b1b1 B2B2 HdHd*, where *B2* largely suppresses awn development and *Hd* results in slight further suppression as well as causing the awnlet to be recurved into a hook or "hood." *Hd* is located on chromosome VIII. *B2* evidently lies on chromosome X. The fact that deficiency for chromosome IX, which is known to carry the factor *b1*, results in an increase in awn development suggests that this recessive gene functions in the same manner as its dominant allele but less actively. Whether *b2* may be of this type also cannot be ascertained, since no *b2b2* material is available for comparison with nullisomic X. Two previously unknown factors affecting awns are indicated by the complete awnlessness of nullisomics II and XX. These factors are of opposite type to the other known awn genes, in that they promote awn development rather than inhibit it.

Characteristics of monosomic plants

Under the most favorable conditions of environment, few of the monosomics corresponding to the 17 different nullisomics differ appreciably from normal. Monosomic IX, which represents the heterozygous speltoid condition, shows the typical speltoid effect of thicker, tougher glumes, as well as lax, tapering, non-"squarehead" spikes. Monosomic XVIII is of distinctly later maturity than normal.

Under less favorable environmental circumstances there may be observed some departure from the normal phenotype in the direction of the nullisomic. The amount of this departure seems to depend upon the degree of the difference between the particular nullisomic and the normal. Thus mono-I plants are seldom distinguishable from normal, while mono-II may deviate so far as to be practically awnless and largely female sterile. So far as has been observed, the monosomic exhibits no peculiarity which does not appear to an exaggerated degree in the nullisomic.

The tendency of monosomic plants to resemble their corresponding nullisomics accounts for the fact that certain monosomics among the immediate offspring of the original monoploid were somewhat abnormal (SEARS 1939), for this family was raised to maturity in the greenhouse under rather crowded conditions. In the next generation, which was grown in the field under favorable conditions, certain monosomes were also reported to cause reduced vigor; but only abnormal-appearing plants were examined cytologically in these families. These plants happened to be monosomic, as presumably were most of the plants classed as phenotypically normal. The statement concerning the progeny from plant 2, that "the only monosomic which occurred was dwarfed and sterile," has proved upon re-examination of the cytological preparation obtained from this plant to have been incorrect. The plant was definitely nullisomic (for chromosome II), and its sibs, which were classed as normals on phenotypic grounds, were presumably mostly monosomic. The seed from two sibs has since been grown, and these two plants were both monosomic.

Transmission of monosomes

Since the transmission of monosomes results in normal rather than monosomic or nullisomic offspring, it is less confusing to speak of the transmission of the deficiencies concerned. Thus, it may be said that mono-I plants have deficiency I and that this deficiency is transmitted by means of deficient-I gametes to the mono- and nulli-I offspring.

When monosomic plants are selfed, nullisomic offspring are produced in frequencies ranging from about one to ten percent. In table 1 are presented the data available concerning the frequency of occurrence of each of the 17 nullisomics. The data are less accurate for some nullisomics than for others, because classification of nullisomics was sometimes made without cytological examination, frequently at the seedling stage. This procedure introduced at least two sources of error: (1) The difficulty of separating certain nullisomics from monosomic or normal sibs at seedling stages. This is particularly true of nullisomics I, VII, and XI, and, under certain conditions, of nullisomics II, XVII, XIX, and XX. (2) The resemblance to nullisomics shown by certain plants with a telocentric or iso-monosome. This phenomenon, which is due to the fact that most or all of the factors on a particular chromosome affecting the morphology of the plant may be located on one arm of that chromosome, has been observed for chromosomes II, III, IV, VI, IX, and X. It will be noted that these two sources of error operate in opposite directions, the first tending to decrease the number of nullisomics recorded (since seedlings classified as

TABLE 1

Frequency of nullisomics in progenies from self-pollinated monosomics.

MONOSOME INVOLVED	NUMBER SEEDS PLANTED	NUMBER PLANTS OBTAINED	PERCENTAGE NULLISOMIC
I	403	393	1.8
II	669	613	6.4
III	1027	1009	10.3
IV	977	933	6.3
V	968	937	0.9
VI	160	153	4.6
VII	50	49	4.1
VIII	110	108	2.8
IX	135	134	1.5
X	290	278	1.8
XI	205	199	2.5
XV	1263	1232	6.2
XVI	726	712	5.8
XVII	300	296	3.0
XVIII	503	492	1.0
XIX	305	293	3.1
XX	190	187	3.7

non-nullisomic were discarded), and the second tending to increase the number recorded. On the whole, the data are believed to be reasonably reliable. Particularly trustworthy are the figures for the three nullisomics which occurred least frequently, V (0.9 percent), XVIII (1.0 percent), and IX (1.5 percent). The value for the most frequently occurring nullisomic, III (10.3 percent), is also probably fairly accurate.

The observed frequencies of nullisomics are of the same order as those previously reported for nullisomics in wheat (HUSKINS 1928; NISHIYAMA 1928). In hexaploid oats, however, PHILP (1935, 1938) found two nullisomics which appeared in frequencies of up to 85 percent among the offspring of monosomics.

The relatively few data available on the separate male and female transmission of whole-chromosome deficiencies suggest that female transmission is about 75 percent, regardless of the chromosome concerned, and that male transmission varies from approximately 1 to 15 percent, depending on the chromosome. On the female side, 39 gametes analyzed from monosomic II showed 74 percent to be deficient, 32 from III showed 81 percent deficient, 20 from XV showed 70 percent deficient, and 23 from XVI showed 70 percent deficient. On the male side, 57 gametes from mono-I showed 5 percent deficient, 26 from III showed 19 percent deficient, and 23 from XVI showed 9 percent deficient. For the chromosomes concerned, these amounts of male transmission, coupled with about 75 percent female transmission, account reasonably well for the observed frequencies of nullisomics.

Data available on the proportion of monosomics among the non-nullisomic

plants in the progenies of monosomics tend to bear out the conclusions reached concerning transmission. The proportion of monosomics has varied approximately from 75 to 85 percent, with the higher values attributable to a selection of monosomics over normals for examination.

The transmission data agree reasonably well with those of NISHIYAMA (1928), who found 73 and 11 percent of functioning deficient female and male

TABLE 2

Chromosome constitution of the offspring of nulli-III plants pollinated by normals.

CONSTITUTION		NO. PLANTS OF SPECIFIED CONSTITUTION			
NO. MONOSOMES (IN ADDITION TO MONO-III)	NO. TRISOMES	IN POPULATION 1	IN POPULATION 2	IN POPULATION 3	IN POPULATION 4
0	0	54	44	45	74
1	0	24	17	25	18
2	0	4	1	6	2
3	0	0	1	2	0
0	1	9*	5	3	2
0	2	3	0	1	0
0	3	1	0	0	0
1	1	1	1*	1	1
1	2	0	0	2	0
2	1	0	1	3	0
2	3	0	0	1	0
3	2	0	0	1	0
Total		96	70	90	97
Inviable seeds		6	19	6	10

* Includes one secondary trisome.

gametes, respectively, from monosomic-"g" plants. From monosomic "f" he reported 71 and 37 percent of deficient female and male gametes, but the figure for male transmission is probably too high, for only 14 percent of nullisomics were obtained from selfing monosomic-"f" plants.

No evidence has been found of any selection against n−1 female gametes, such as was observed by GREENLEAF (1941) in *Nicotiana Tabacum*.

The preponderance of deficient female gametes is attributable to the frequent elimination of the univalent monosome through its failure to be included in a daughter nucleus at the reduction division. The low number of functioning deficient male gametes is presumably due to the considerable elimination of deficient pollen through competition with normal pollen.

The origin of monosomes from nulli-III plants

As mentioned previously, nullisomic-III plants are characterized by the presence in most MI microsporocytes of two or more univalent chromosomes. As shown in figure 1, there seems to be a general reduction in chiasma fre-

quency. Despite this abnormality, however, fertility is good, sometimes, reaching 100 percent in the more vigorous spikes. Functioning female gametes, all of which are of course deficient for chromosome III, may carry no additional abnormalities or may be deficient for as many as two or three additional chromosomes and duplicated for two or three others. Table 2 shows the constitution of the offspring of nulli-III plants pollinated by normals in four dif-

TABLE 3

Frequency of various monosomes in the progeny of nulli-III plants.

MONOSOME	FREQUENCY IN POPULATION 1	FREQUENCY IN POPULATION 2	TOTAL FREQUENCY
I	0	1	1
II	4	1	5
IV	12	2	14
V	0	1	1
VI	2	0	2
VII	2	1	3
IX	1	4	5
X	1	0	1
XI	0	1	1
XV	4	6	10
XVII	2	1	3
XVIII	3	0	3
XIX	0	2	2
XX	0	2	2
Lost	1	1	2
Unidentified	1	2	3
Totals	33	25	58

ferent seasons. Among 353 plants grown, 136 were aberrant. These 136 plants had 138 monosomes and 47 trisomes.

It appears from table 2 that the frequency of aberrant plants among the offspring of nullisomic III may vary from season to season. Population 4 had only 23.7 percent aberrant plants, while the average for the other three populations was 44.1 percent. This accords with the observation that the frequency of univalents in nulli-III plants is sometimes relatively low, particularly in exceptionally vigorous plants.

There also appears to be a tendency for certain chromosomes to occur unduly frequently as monosomes among the offspring of nulli-III. This is shown in table 3, which gives the frequency with which the various monosomes occurred in populations 1 and 2. Monosome IV occurred 14 times and mono-XV occurred ten times in the total of 58 monosomes in the two populations. Since there are 20 possible monosomes (excluding III), the mean frequency is 2.9 $\pm$ 1.66. Mono-XV therefore deviated from expectation by about four times the standard error, and mono-IV by more than six times the standard error—both highly significant values.

The high frequency of occurrence of monosomes IV and XV in offspring of nulli-III seems best attributed to a correspondingly frequent occurrence of these chromosomes as univalents in nulli-III. Presumably the tendency to pair may be affected by chromosome length, but other factors must operate as well. Chromosome XV is very short, but so is XIX, which occurred only twice. Whatever the factors determining which chromosomes shall pair when there is a tendency for a reduced frequency of chiasmata, such as in nullisomic III, the variation thereby effected would be expected to cause some monosomes to arise with unduly high frequency and others with unduly low frequency. Numbers are too small as yet to show whether or not the latter class exists.

TRISOMES AND TETRASOMES

Duplications as a rule affect viability less than do deficiencies, and it is therefore not surprising that $2n+1$ types have been found in various species much more frequently than have $2n-1$ types. Similarly, tetrasomic types ($2n+2$) are apparently more easily obtained than nullisomics. Six of the twelve possible tetrasomics in *Nicotiana sylvestris* have been isolated (GOODSPEED and AVERY 1939), while nullisomics apparently cannot be obtained either in this species or in the more highly polyploid species *N. Tabacum*, which is evidently an amphidiploid of *N. sylvestris*×*N. tomentosa* (CLAUSEN 1941b).

In wheat, tetrasomics have not been reported as often as nullisomics, presumably because they and the trisomic types from which they are derived occur less frequently than nullisomics and monosomics and have not been so easily distinguished phenotypically from normal. WINGE (1924) reported that homozygous speltoids were tetrasomic for one chromosome and nullisomic for another. HUSKINS (1928) described a similar situation for certain homozygous speltoids and reported others which were simply tetrasomic. BYNOV (1938b) found 44 chromosomes in homozygous speltoids, these presumably being tetrasomic. A short-compactum type was reported by UCHIKAWA (1937) to be tetrasomic. HUSKINS (1931) found that the unfixable dwarf of VILMORIN (1913) was trisomic and that the occasional extreme dwarf offspring were tetrasomic. Possibly the dwarfs reported by some of the other early investigators were also trisomic or tetrasomic types.

From the five trisomes present in the progeny of the monoploid, and from the numerous additional ones obtained from nulli-III (table 2), 11 tetrasomes have been obtained. The six of these which have been tested have proved to involve six different chromosomes, but it is probable that there are one or more duplicates of these among the remaining five. Only one has been identified with respect to the chromosome concerned, and that one involves chromosome II.

In general the tetrasomic plants are of more nearly normal phenotype than are nullisomics. Only one is of conspicuously reduced vigor and fertility, and that one is both male and female fertile. The fertility of tetra-II is somewhat reduced, but not nearly to the degree of nulli-II, which is female sterile. Tetra-II differs from normal in the opposite direction from nulli-II in most respects:

It tillers more than normal, has narrower culms and leaves, and has longer awns (fig. 2g).

Although tetrasomic plants frequently have quadrivalent configurations at meiosis, chromosome distribution is fairly regular. Among 44 offspring from six tetrasomics of different origin, all but eight were tetrasomic.

Most of the trisomics are little different from normal, except tri-II, which has the characteristics of tetra-II, but to a lesser degree. Tri-IX has tentatively been identified as a type with compact spikes.

The frequency of tetrasomic plants obtained among the offspring of trisomics has been similar to that of nullisomics in progenies of monosomics—that is, from about one to ten percent. It appears, however, that the extra chromosomes are transmitted through fewer female gametes and more male gametes than are the various deficiencies. Perfectly regular meiotic behavior of a trisome can result in only 50 percent of the gametes having an extra chromosome, and irregularities reduce this percentage by causing chromosome losses. The data thus far available indicate a frequency of 40 percent or less of disomic female gametes. With this comparatively low female transmission, male transmission must be somewhat higher than for the deficiencies.

COMPENSATING NULLISOMES AND TETRASOMES

Two instances have been found where a particular tetrasome cancels in part or almost entirely the effects of a certain nullisome, and one compensating trisome-nullisome combination has also been found. Similar compensating combinations have been reported by HUSKINS (1941) in both wheat and oats.

The combination tetra-II, nulli-XX is very nearly normal in all respects (fig. 2e), including fertility, although both tetra-II (fig. 2g) and nulli-XX (fig. 2a) are markedly abnormal. The compensation apparently extends to the male gametophyte, for preliminary data indicate no competitive advantage for normal pollen over pollen duplicated for chromosome II and deficient for chromosome XX. Of 39 offspring of a tri-II, mono-XX plant, none were of normal constitution, eight were tetra-II and nulli-XX, and the rest were of such constitution as not to permit identification of the gametes which produced them. Assuming that 75 percent of the germ cells were deficient for chromosome XX and that 36 percent were duplicated for II, 27 percent would be both deficient-XX and duplicated-II, and 16 percent would be normal. The other two types of gamete, which are not involved in the production of the critical plants, may be omitted from consideration on the male side, since presumably they are largely eliminated by pollen competition. In the absence of any competitive advantage for normal pollen over the duplicated-deficient type, six percent normal plants and 17 percent nulli-XX, tetra-II plants would then be expected—approximately a 1:3 ratio. An advantage for normal pollen would increase the proportion of normal plants. The fact that no normal plants and eight nulli-XX, tetra-II plants occurred out of 39 conforms reasonably well to expectation on the basis of no advantage to normal pollen. The deviation, in fact, is in the opposite direction, though not significantly so.

The ability of tetra-II to compensate for nulli-XX suggests that these two chromosomes have one or more segments in common. Further evidence of this is the fact that mono-II, mono-XX plants resemble the parental nullisomics in all respects, including infertility. The common segment is evidently not long, however, for no pairing at meiotic metaphase has been observed between monosomes II and XX or between trisome II and monosome XX.

The other compensating nullisome-tetrasome combination involves nulli-XVI and an unidentified tetrasome. The degree of compensation is not sufficient to result in normal plants, but it does decidedly improve the vigor and fertility of nullisomic-XVI. As with the II–XX combination, no tendency has been found for the two chromosomes to pair. Deficient-duplicated pollen apparently competes rather favorably with normal pollen. Of 15 male gametes from a monosomic-trisomic plant tested in a cross with a normal plant, six were deficient-duplicated and nine were normal. Comparison of this 6:9 distribution with the approximate 9.4:5.6 ratio expected in the absence of selection shows a deviation toward selection of normal pollen, but this deviation is not significant statistically.

The nullisome-trisome combination mentioned involves nulli-I and shows nearly perfect compensation. The combination originated when the trisome arose in a nullisomic-I line. No offspring have been grown.

Because of the favorable competitive position of $n-1+1$ pollen in which the duplicated chromosome tends to compensate for the missing one, there is selection in favor of compensating combinations. Hence, compensating nullisome-tetrasome combinations tend to appear with undue frequency. Several non-compensating combinations, however, have been obtained by crossing nullisomics with tetrasomics.

TELOCENTRICS AND ISOCHROMOSOMES

Recent work of UPCOTT (1937) and DARLINGTON (1939) has shown that univalent chromosomes, through misdivision of the centromere, may give rise to telocentric chromosomes, which are completely deficient for one arm, or to isochromosomes, which are deficient for one arm and duplicated for all of the other arm. Secondary aberrations of both these types occur in the offspring of trisomic and particularly of monosomic plants of *Triticum vulgare*. Either a telocentric or an isochromosome or both has been obtained for one or both arms of 15 of the 17 identified monosomes.

The frequency of telocentrics and isochromosomes among the offspring of certain monosomics appears to be rather high. For example, among 146 daughter plants of monosomic-VI grown in the 1940–41 season, two had a telomonosome and three had an isomonosome. In all five of these plants, which closely resembled nullisomics, the same arm of chromosome VI was involved. Since only 15 plants, mostly resembling nullisomics, were examined cytologically in this population, it is possible that several other individuals possessed telo- or isomonosomes for the other arm of VI, or telocentrics or isochromo-

somes for either arm in company with a normal chromosome. All of these types would presumably have been practically normal in appearance.

It is probable that the frequent occurrence of telocentrics and isochromosomes in the progeny of monosomics results primarily from pollen competition rather than from a high frequency of misdivision. Normal pollen has a strong competitive advantage over nullisomic pollen, and pollen deficient for only part of a chromosome should have a somewhat similar advantage, particularly if the majority of genes affecting gametophytic development happened to be located on the arm which was present. This selective advantage dependent on the proportion of important genes on the remaining arm would account for the differing frequencies with which telocentrics and isochromosomes involving different chromosomes and different arms of the same chromosome appear. It is not unlikely, however, that differences in the frequency of misdivision also occur.

The behavior of telocentrics and isochromosomes at meiosis and mitosis will be the subject of a subsequent paper. It may be stated here, however, that telocentrics in *T. vulgare* are sometimes lost in somatic tissue and that isochromosomes apparently may lose one arm or be entirely lost. RHOADES (1940) found that a telocentric chromosome in maize was occasionally lost or modified in somatic tissue, but that the corresponding isochromosome apparently behaved normally.

DISCUSSION

Although *Triticum vulgare* is an allo- rather than an autopolyploid, there is evidently considerable duplication in its chromatin. Numerous sets of duplicate factors are known; and STADLER (1929) found fewer mutations following X-ray treatment of the hexaploid *T. vulgare* than following treatment of diploid and tetraploid wheats, indicating that many gene loci are covered up by duplicate genes at other loci. Cytological evidence of duplication is also available, in that up to five pairs of chromosomes may occur at meiosis in monoploids.

There is as yet little indication as to how large a fraction of the total amount of chromatin is duplicated, nor how this duplicated chromatin is distributed among the chromosomes. The cytological data from the monoploids, where frequently no pairs and usually not more than one are found, show that no two chromosomes are homologous throughout their length and suggest that there is altogether little duplication. However, there is reason to believe that cytological data cannot be depended on to reveal inter-chromosomal homologies which involve short segments of chromatin. Several instances are known in which a tetrasome is able to compensate partially for a certain nullisome, but no tendency has been detected for the presumably homoeologous chromosomes to be associated at meiosis. Furthermore, the viability of the various nullisomic types suggests that the amount of duplication which exists may be much greater than indicated by the pairing in monoploids. Obviously

the nullisomics would not be viable unless every essential gene were duplicated in other chromosomes.

In *Nicotiana Tabacum*, an allotetraploid with 24 pairs of chromosomes, nearly all of the possible different monosomics have been obtained and several of these have been rather extensively tested, but none has given rise to a nullisomic (OLMO 1935; CLAUSEN 1941a, b). Similarly, LAMMERTS (1932) was unable to obtain the nullisomic types from seven different monosomics in *N. rustica* (n=24). The failure of nullisomics to appear in these two Nicotiana species is evidently due primarily to inviability of nullisomic zygotes, since several types of 23-chromosome pollen have proved functional to some extent. The contrast with *T. vulgare* is explainable by the fact that *vulgare* is a hexaploid rather than a tetraploid like tobacco, and therefore presumably has more duplication. In connection with this problem, certain of the deficiencies in *T. vulgare* are being transferred to a tetraploid wheat, where their effects both as monosomes and nullisomes (if obtainable) can be compared with their effects in the hexaploid.

For the genetic analysis of polyploid species, the nullisomic method is highly advantageous. Dominant or partially dominant factors, whether previously known or not, can be located on the chromosomes simply by observation of nullisomic plants. Recessive factors can be located by crossing each nullisomic to a strain carrying the dominant allele and observing the F_2's for departures from a 3:1 ratio. The critical F_2 will show the recessive condition only in the occasional nullisomic plants. Where ratios tend to be obscured by the segregation of duplicate factors or modifiers, or where classification is difficult, backcrosses of the F_1 can be made to the respective nullisomics until in each case all but the desired one of the chromosomes of the variety being tested are eliminated. The effects of the various chromosomes can then be compared against a uniform background. This method should prove particularly suitable for the location of factors for resistance to certain diseases, where reactions of individual plants may not be entirely trustworthy.

The chromosomal aberrations also yield information as to the action of certain genes. For example, the factor *B2* on chromosome X has been considered a dominant inhibitor of awns, because in most crosses *B2b2* resembled *B2B2* more closely than it did *b2b2*. This fact, however, fits equally well the theory that *B2* is without effect and *b2* promotes awn development, with a threshold effect such that two doses of *b2* result in awns more than twice as long as does one dose of *b2*. But the nullisomic decides in favor of the inhibitor hypothesis, since nulli-X is awned. The comparable gene *b1*, located on chromosome IX, even has a slight inhibitory action on awn development, as shown by the somewhat longer awns of nulli-IX than of *b1b1*.

Where both the nullisomic and the tetrasomic have been obtained for a particular chromosome, as for chromosome II, a series is made available in which the chromosome is present in doses of from 0 to 4, inclusive. Such a series may be used advantageously to measure the dosage effect of genes located on that chromosome.

SUMMARY

Seventeen of the 21 possible nullisomics in *Triticum vulgare* var. Chinese Spring have been obtained. Eleven of these (designated I to XI) involve chromosomes homologous to those of the emmer or tetraploid wheats, while the remaining six (XV to XX) involve chromosomes not represented in the emmers. All are reduced in vigor to various degrees, but all mature, and none is completely sterile. Nulli-III is partially asynaptic and has been used as a source of additional aberrations.

The location of several genetic factors is revealed by the nullisomics: A factor for red seeds on chromosome XVI, the hooded factor (*Hd*) for recurved awns on VIII, the awn suppressor *B2* on X, and factors for promotion of awn growth on II and XX. The speltoid chromosome, with factors for pubescent nodes, squareheadedness, and suppression of awns, is IX. The recessive *b1* on chromosome IX, whose dominant allele inhibits awns, also inhibits awns to a small extent.

Nullisomics have been recovered in frequencies of less than one to more than ten percent in the progenies of monosomics. The differences depend mainly on the elimination of different proportions of the deficient pollen. Apparently about 75 percent of functioning female gametes are deficient regardless of the chromosome concerned.

Tetrasomics have occurred among the offspring of trisomics in frequencies of about one to ten percent. One tetrasome involves chromosome II and compensates almost completely for nullisome XX. Another tetrasome compensates partially for nulli-XVI, and a certain trisome largely compensates for nulli-I.

Telocentrics and isochromosomes occur fairly frequently among the offspring of monosomic plants, following misdivision of the univalent chromosome.

ACKNOWLEDGMENT

The writer is indebted to DR. L. J. STADLER for encouragement and advice received at various stages of the investigation.

LITERATURE CITED

BYNOV, F. A., 1938a Mutations in *Triticum vulgare* produced by the action of an electric current. Trav. Jard. Bot. Univ. Moscow **2**: 17–35.

1938b Centrifuging as a factor in mutation. Trav. Jard. Bot. Univ. Moscow **2**: 36–46.

CLAUSEN, R. E., 1941a Monosomic analysis in *Nicotiana Tabacum*. Genetics **26**: 145.

1941b Polyploidy in Nicotiana. Amer. Nat. **75**: 291–309.

CUTLER, G. H., 1919 A dwarf wheat. J. Amer. Soc. Agron. **11**: 76–78.

DARLINGTON, C. D., 1939 Misdivision and the genetics of the centromere. J. Genet. **37**: 341–364.

FARRER, W., 1898 The making and improvement of wheats for Australian conditions. Agric. Gaz. New South Wales **9**: 152–156.

GOODSPEED, T. H., and P. AVERY, 1939 Trisomic and other types in *Nicotiana sylvestris*. J. Genet. **38**: 381–458.

GREENLEAF, W. H., 1941 The probable explanation of low transmission ratios of certain monosomic types of *Nicotiana Tabacum*. Proc. Nat. Acad. Sci. **27**: 427–430.

HÅKANSSON, A., 1930 Zytologische Beobachtungen an s. g. Speltoidheterozygoten beim Weizen. Svensk Bot. Tidskr. **24**: 44–57.

HUSKINS, C. L., 1927 On the genetics and cytology of fatuoid or false wild oats. J. Genet. **18**: 315–364.

1928 On the cytology of speltoid wheats in relation to their origin and genetic behavior. J. Genet. **20**: 103–122.

1931 A cytological study of Vilmorin's unfixable dwarf wheat. J. Genet. **25**: 113–124.

1941 Polyploidy and mutations. Amer. Nat. **75**: 329–344.

KIHARA, H., 1924 Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, **1**: 1–200.

LAMMERTS, W. E., 1932 Inheritance of monosomics in *Nicotiana rustica*. Genetics **17**: 689–696.

LOVE, R. M., 1940 Chromosome number and behaviour in a plant breeder's sample of pentaploid wheat hybrid derivatives. Canad. J. Res., C, **18**: 415–434.

MATSUMURA, S., 1939 Das fehlende Chromosom beim B-Speltoidweizen. Japan. J. Genet. **15**: 323–324.

NEETHLING, J. H., 1917 A preliminary note on dwarfs appearing in Gluyas Early (wheat) hybrids. S. Afr. J. Sci. **14**: 540–547.

NISHIYAMA, I., 1928 On hybrids between *Triticum spelta* and two dwarf wheat plants with 40 somatic chromosomes. Bot. Mag. Tokyo **42**: 154–177.

OLMO, H. P., 1935 Genetical studies of monosomic types in *Nicotiana Tabacum*. Genetics **20**: 286–300.

PHILIPTSCHENKO, J., 1929 Ein neuer Fall von Speltoidmutationen beim Weizen. Z. i. A. V. **52**: 406–413.

PHILP, J., 1935 Aberrant albinism in polyploid oats. J. Genet. **30**: 267–302.

1938 Aberrant leaf width in polyploid oats. J. Genet. **36**: 405–429.

RHOADES, M. M., 1940 Studies of a telocentric chromosome in maize with reference to the stability of its centromere. Genetics **25**: 483–520.

RICHARDSON, A. E. V., 1913 Wheat and its cultivation. Victoria Dept. Agric. Bull. **22**: 115–116.

SEARS, E. R., 1939 Cytogenetic studies with polyploid species of wheat. I. Chromosomal aberrations in the progeny of a haploid of *Triticum vulgare*. Genetics **24**: 509–523.

1941 Nullisomics in *Triticum vulgare*. Genetics **26**: 167–168.

1944 The amphidiploids *Aegilops cylindrica*×*Triticum durum* and *A. ventricosa*×*T. durum* and their hybrids with *T. aestivum*. J. Agric. Res. **68**: 135–144.

STADLER, L. J., 1929 Chromosome number and the mutation rate in Avena and Triticum. Proc. Nat. Acad. Sci. **15**: 876–881.

THOMPSON, W. P., 1922 Lethal factors in cereals. Proc. W. Canad. Soc. Agron. **3**: 53–59.

1928 The genetics and cytology of a dwarf wheat. Trans. Roy. Soc. Canada, Ser. 3, Sect. 5, **22**: 335–349.

UCHIKAWA, I., 1937 Cytogenetic studies on compactoid wheat. Japan. J. Genet. **13**: 9–15.

1938 Cytogenetic studies on short-normal type and dwarf compactum type in compactoid mutation. Japan. J. Genet. **14**: 264–267.

UPCOTT, M., 1937 The external behaviour of the chromosomes. VI. The behaviour of the centromere at meiosis. Proc. Roy. Soc., B, **124**: 336–361.

VILMORIN, P. DE, 1913 Sur une race de blé nain infixable. J. Genet. **3**: 67–76.

WALDRON, L. R., 1924 A study of dwarfness in wheat accompanied by unexpected ratios. Genetics **9**: 212–246.

WATKINS, A. E., and S. ELLERTON, 1940 Variation and genetics of the awn in Triticum. J. Genet. **40**: 243–270.

WINGE, Ø., 1924 Zytologische Untersuchungen über Speltoide und andere mutantenähnliche Aberranten beim Weizen. Hereditas **5**: 241–286.