CYTOGENETIC STUDIES WITH POLYPLOID SPECIES OF WHEAT. I. CHROMOSOMAL ABERRATIONS IN THE PROGENY OF A HAPLOID OF TRITICUM VULGARE[1]

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INTRODUCTION

THE usual methods of genetic analysis lose much of their efficiency when applied to polyploid organisms, where duplicate factors tend to mask recessive gene mutations, and where the large number of chromosomes greatly increases the difficulty of determining linkages. A different way of analyzing polyploids is being tried with *Triticum vulgare.* This method is based on the fact that whole-chromosome deficiencies and duplications are viable in *T. vulgare,* and that these aberrations, as well as reciprocal translocations, can be obtained from haploids of this polyploid species. The origin and possible uses of two reciprocal translocations and a number of whole-chromosome aberrants from a haploid of *T. vulgare* will be discussed in this paper.

PROGENY OF A HAPLOID WHEAT PLANT

Two haploids were found in a field culture of 105 plants grown from seed of *T. vulgare* var. "Chinese Spring" ($n=21$) pollinated by *Secale cereale* ($n=7$). They were not conspicuously different from diploid Chinese Spring wheat, except for complete male sterility. One of the haploids was completely female sterile, but the other set 14 seeds from less than 300 florets pollinated by normal wheat pollen, and nine seeds from a somewhat larger number of florets pollinated by rye. Successful pollinations involved several different spikes from various parts of the plant, and were made over a period of about two weeks.

From the nine seeds of the haploid pollinated by rye, two mature plants were obtained. These had 27 and 28 chromosomes, respectively, and resembled ordinary wheat-rye hybrids. Neither plant produced seeds.

The 14 seeds of the haploid pollinated by diploid wheat yielded 13 mature plants. Cytological examination at meiosis in these plants, supplemented by similar studies of their progeny, provided the information given in table 1. The aberrant chromosome numbers and pairing relationships of plants 1 to 11 presumably resulted from abnormal chromosome consti-

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tution of the eggs produced by the haploid. Although no study was made of microsporogenesis in the plants used as pollen parents, several other diploids of Chinese Spring wheat showed regular meiotic behavior. At least two different individuals were involved in the male parentage of the aberrant plants.

TABLE I

Results of cytological analysis of the progeny of a cross, Triticum vulgare haploid × T. vulgare diploid.

DESIGNATION OF PLANT	SOMATIC NUMBER	BIVALENTS	UNIVALENTS	TRIVALENTS*	RINGS OF FOUR
1	41	20	1		
2	41	20	1		
3	41	20	1		
4	41	20	1		
5	41	20	1		
6	42	19	1	1	
7	40	19	2		
8	41	18	2	1	
9	41	18	2	1	
10	40	17	2		1
11	42	15	2	2	1
12	42	21			
13	42	21			

* Trivalents were frequently replaced by a bivalent and a univalent.

DESCRIPTION OF THE ABERRANT PLANTS AND THEIR PROGENY

Selfed seeds were obtained from all the aberrant plants but one. Some individuals were abundantly fertile under bag, while others had to be pollinated by hand. The poorly self-fertile plants, including the one which had set no seeds, were later back-pollinated successfully by normal Chinese Spring wheat.

Plants with a single univalent

Five individuals were characterized at meiosis by the presence of twenty pairs of chromosomes and one univalent.

In the following descriptions, numbers given to plants correspond to those in table 1.

1. Plant number 1 showed a slight chlorophyll defect. From 20 selfed seeds, 20 plants were obtained, of which two and possibly a third were monosomic, and two were nullosomic (20 pairs of chromosomes). The monosomic plants under field conditions were somewhat smaller and less vigorous than disomic sibs, and were lighter in color. The nullosomics were bushy dwarfs with stiff leaves more nearly normal in color than those of the monosomics. Neither of the nullosomic plants set seeds, but enough

functional pollen was obtained from one of them to produce a viable seed in a cross to *T. durum*.

2. Plant number 2, grown under greenhouse conditions, was nearly normal, differing mainly in the greater thickness and stiffness of its culms. Among its field-grown progeny, however, the only monosomic which occurred was dwarfed and sterile. The 28 plants (from 30 selfed seeds) included no nullosomics.

3. This monosomic was somewhat defective in size and vigor, although normal in color. From 20 selfed seeds, 16 plants were obtained, including three monosomics and no nullosomics. The aberrant plants resembled their parent in size and vigor.

4. This plant did not differ noticeably from normal, but in the field its monosomic offspring were somewhat lighter in color. Of 34 plants which resulted from 35 selfed seeds, three were found by cytological examination to be monosomic, and several which were not studied cytologically had the characteristic color of monosomics. No nullosomics were observed.

5. This was a rather small, weak plant, which did not set selfed seed until late in the season. Two daughter plants were obtained from four backcrossed seeds, and both were monosomic. These were more vigorous than the parent.

Plant with one univalent and one trivalent

6. No differences from the normal could be detected in plant number 6, nor could the monosomic and trisomic plants in its progeny be identified other than cytologically. From 16 selfed seeds, 16 plants resulted. Of the 15 of these which were studied cytologically, only two were normal, six were monosomic (figure 1), five had one univalent and one trivalent (figure 4), one had a univalent and a quadrivalent (figure 5), and one was nullosomic. The nullosomic plant, although small and lacking in vigor, had normal pollen fertility and set a number of selfed seeds. The monosomic-tetrasomic plant was normal, or nearly so, in appearance and fertility.

Plant with two univalents

7. This plant had narrow leaves and slender spikes and culms. From seven selfed seeds, six plants were obtained, of which five were examined cytologically. Four were of the parental constitution (figure 2), although phenotypically nearer normal, while the fifth had 20 bivalents and one univalent.

Plants with two univalents and one trivalent

8. This was the smallest and weakest of the 11 plants. It had a very short spike and shed no pollen. The only plant obtained from the three

backcrossed seeds had one univalent and one trivalent, and was much more vigorous than its parent.

9. This individual had a glossy appearance, and produced a short tapering spike with an extra spikelet at each of several central nodes. Two selfed seeds were obtained, and these produced one plant of the parental constitution (figure 3) and one with a single univalent. A single backcrossed seed gave an individual with one univalent and one trivalent.

Plant with two univalents and a ring of four

10. This plant was characterized by a dark green striping of its leaves. From 22 selfed seeds 21 plants were obtained, of which all but six were studied cytologically. Three were of the parental constitution (but failed to show the stripe), seven had one univalent and a ring of four, one had one univalent and a chain of four, three had two univalents, and one had one univalent. Figure 6 shows the appearance of the ring at first metaphase.

Plant with two univalents, two trivalents, and a ring of four

11. This plant was not conspicuously abnormal, its chief distinctive characteristic being a glossy appearance. Three plants were obtained from three selfed seeds, and two of these were examined cytologically. One, which died without setting seed, had two univalents, one trivalent, and a ring of four. The other plant had a trivalent and a chain of four. From 11 backcrossed seeds, 10 plants resulted. Two of these had two univalents and two trivalents; one had two univalents, one trivalent, and a ring of four; two had two univalents and one trivalent; one had one univalent, one trivalent, and a ring of four; one had one univalent, one trivalent, and a chain of four; two had one univalent and one trivalent; and one was normal.

EXPLANATION OF PLATE

Photographs from aceto-carmine smears, showing first metaphases (except figure 3) in aberrant plants. ×850.

FIGURE 1.—A monosome with a conspicuous, sub-terminal constriction, from an offspring of plant 6.

FIGURE 2.—Two monosomes, one considerably longer than the other, from an offspring of plant 7.

FIGURE 3.—Two monosomes at first anaphase, showing the chromatids passing to the poles. The upper chromosome has a median centromere, the lower a sub-terminal centromere. From an individual in the progeny of plant 9.

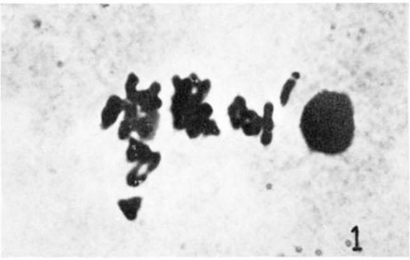
FIGURE 4.—A trisome, from an offspring of plant 6.

FIGURE 5.—A tetrasome (at left), from an offspring of plant 6.

FIGURE 6.—A ring of four, from an offspring of plant 10.

FIGURE 7.—Thirteen bivalents and eight univalents in a 34-chromosome hybrid of *T. durum* with a monosomic offspring of plant 3. u = univalent.

FIGURE 8.—Fourteen bivalents and six univalents in a 34-chromosome hybrid of *T. durum* with a monosomic offspring of plant 10.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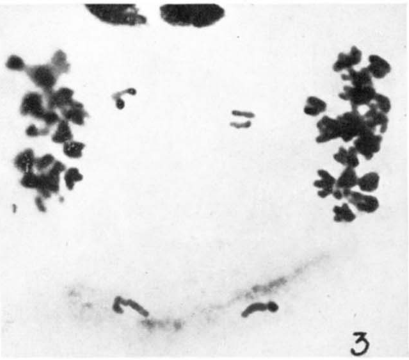
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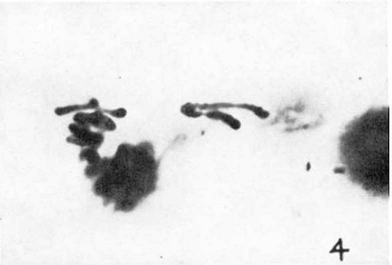
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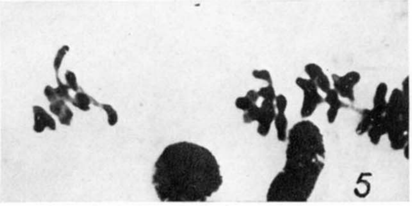
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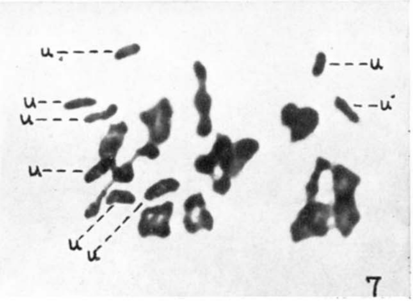

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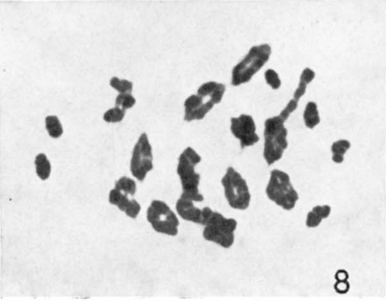
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GENERAL CONSIDERATION OF THE ABERRATIONS

Monosomes

In the chromosome constitutions of the 11 aberrant plants in the immediate progeny of the haploid, 16 monosomes were involved, of which two were lost in the succeeding generation. Where two of these occurred in the same plant, as they did in five instances, those two necessarily involved non-homologous chromosomes; and other differences between the monosomes have been indicated by differences in appearance of monosomic plants and by differences in the size and morphology of the chromosomes concerned (figures 1, 2, 3). The chance of all 14 monosomes being different is small, however, even though they may have occurred at random.

The effort involved in determining homologies amongst the 14 monosomes would be much less if there were reliable cytological means of identifying the chromosomes. Recent work of BHATIA (1938) indicates that cytological distinctions do exist among most of the chromosomes.

Since the 14 chromosomes of emmer wheats pair regularly with 14 of the 21 *vulgare* chromosomes (SAX 1922), a 34-chromosome hybrid of emmer with a monosomic plant of *T. vulgare* will show at meiosis whether or not the monosome concerned is a chromosome homologous with one of emmer. Of eight monosomes thus far tested, five (figure 7) have proved to have a homolog in the emmer complement, while three (figure 8) are among the extra seven chromosomes of *T. vulgare*. *T. durum* was the emmer wheat used.

Deficiencies of whole chromosomes or parts of chromosomes have been observed several times in 21-chromosome wheats. KIHARA (1924) obtained in the F_4 of a cross between *T. polonicum* and *T. spelta* two plants which had only 20 pairs of chromosomes and which bred true. One was a dwarf with a somewhat lowered seed set, while the other was semi-dwarf, with nearly normal fertility. NISHIYAMA (1928) studied the monosomic plants which were obtained from these two lines through crosses with normal plants. He found that such monosomics produced functioning 20-chromosome gametes, though the proportion was much lower among male than among female germ cells.

HUSKINS (1928, 1933) and HUSKINS and SPIER (1934) have shown that certain types of speltoids are due to deficiency of a whole chromosome or a part of a chromosome. Where a whole chromosome is missing in the speltoid, homozygotes (that is, nullosomics) are rarely obtained, although selfing gives 5 to 20 times as many heterozygotes as normals. Where only a part of a chromosome is missing, homozygous speltoids are more frequently obtained, giving typically ratios near 1:2:1, and sometimes approaching 1:1:1.

UCHIKAWA (1937) also has found 41 chromosomes in a heterozygous speltoid. The same chromosome number was observed in a short, but otherwise normal, plant.

LOVE (1938) showed that white-chaff off-types in a golden chaff wheat were homozygous for a deficiency of one chromosome arm. LOVE (1939) also reports in F_5 to F_7 of *vulgare-durum* crosses *vulgare*-like plants deficient for as many as four chromosomes.

KATTERMANN (1932) isolated 40- and 41-chromosome plants from an F_6 of a wheat-rye cross.

Trisomes

Not as many instances of trisomes in *T. vulgare* have been observed as of monosomes. HUSKINS (1928, 1933) believed that certain speltoids were due to the presence of an extra chromosome or pair of chromosomes. UCHIKAWA (1937) reported that a semi-*compactum* wheat had 43 chromosomes, and its short-*compactum* derivative 44 chromosomes. In *vulgare*-like derivatives of *vulgare-durum* crosses, LOVE (1939) found numerous trivalents, some of which probably represented trisomes.

Thus far, two of the five trisomes obtained from the haploid of *T. vulgare* have been separated from the monosomes which accompanied them in the original offspring of the haploid. Neither differs conspicuously from normal in phenotype. From one trisomic plant both pollen and ovules of $n+1$ constitution have functioned; a daughter plant of a selfed trisomic individual (number 6) was tetrasomic (figure 5).

Reciprocal translocations

The two associations of four[3] observed were presumably reciprocal-translocation configurations rather than tetrasomes. Rings of four occurred with greater regularity than would be expected for tetrasomes, which frequently form a chain of four, or two pairs. Also, since the male parent presumably contributed only one each of the 21 kinds of chromosomes, a tetrasome would necessarily have involved three homologs from the maternal parent. The occurrence of gametes from a haploid with three homologs is difficult to explain.

Additional evidence is available that the ring of four found in plant 10 (figure 6) was due to a reciprocal translocation. The 17 bivalents and two univalents account for only 19 paternal chromosomes, leaving two to be involved in the ring. Furthermore, if the association of four had been a tetrasome, the plant would have been deficient for one pair of chromosomes, in which case it would probably not have been as vigorous as it was.

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[3] There is some evidence from a later generation that a third reciprocal translocation was present in the immediate progeny of the haploid (in plant 7).

The interpretation of the ring of four in plant 11 as a reciprocal-translocation association is substantiated by the pairing relationships in one of its offspring. This daughter plant (from a selfing) had 43 chromosomes, 36 of which always formed 18 pairs. The other seven were observed to form a trivalent and a chain of four; a bivalent, a univalent, and a chain of four; two trivalents and a univalent; a trivalent, a bivalent, and two univalents; or two bivalents and three univalents. Part of this variability can be accounted for by the presence of a trisome, which sometimes formed a trivalent and sometimes a bivalent plus a univalent. The remaining four chromosomes presumably represented an unstable chain of four, which frequently broke up (figure 9) into a trivalent and a univalent, into two bivalents, or into a bivalent and two univalents. Such a chain of

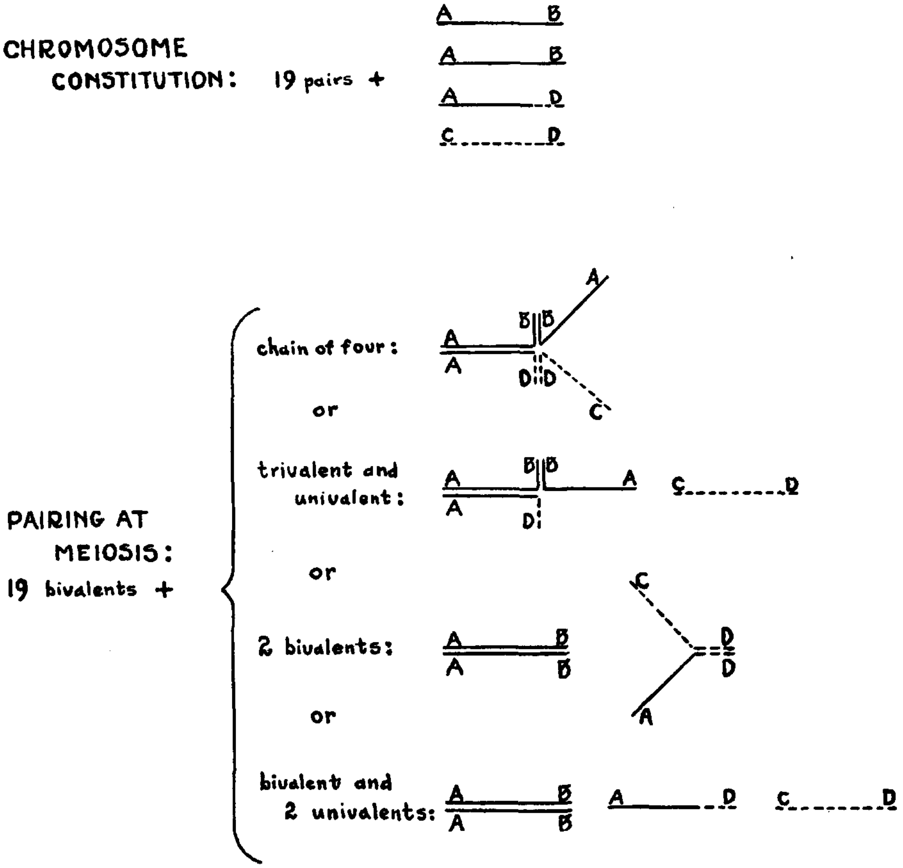

FIGURE 9.—The chromosome constitution and meiotic behavior of a plant which would occur in the progeny of an individual with a ring of four if one of the parental gametes received adjacent chromosomes from the ring and therefore had a duplication and a deficiency.

four would be expected in the progeny of a plant with a reciprocal-translocation ring of four, as a result of the functioning of a duplication-deficiency gamete.

Although neither of the two reciprocal translocations has yet been obtained in a plant which was free from monosomes, it has been possible to determine that they bring about no great reduction in male or female fertility. It is yet to be learned whether this lack of sterility is due mainly to directed segregation of the members of the chromosome ring, as shown by THOMPSON and THOMPSON (1937) in *T. durum* and by these authors (1937) and by SMITH (1939) in *T. monococcum*, or mainly to the ability of deficiency-duplication gametes to survive. In the one instance just discussed the functioning of a deficiency-duplication gamete has been indicated.

A reciprocal translocation in *T. vulgare* has been discovered by KOSTOFF (1937) in a 42-chromosome segregate from a cross of *T. vulgare* × *T. monococcum*. KATTERMANN (1934, 1935a, b) backcrossed a wheat-rye hybrid to wheat and obtained plants with multivalent associations of as many as six chromosomes. Some of these associations probably were due to reciprocal translocations. LOVE (1939) found numerous quadrivalent associations in *vulgare*-like derivatives of *vulgare-durum* crosses.

ORIGIN OF THE ABERRATIONS

Since no cytological study was made of the haploid which produced the aberrant plants, there is no direct evidence as to the mode of origin of the abnormalities. However, the observations of others, particularly of GAINES and AASE (1926) on a haploid of *T. compactum*, suggest several ways in which the aberrations could have arisen.

GAINES and AASE observed usually 21 univalents at first metaphase in their hybrid, although "occasionally two and rarely more" paired. The behavior of the chromosomes at first anaphase varied considerably. Sometimes the univalents were distributed to the two poles more or less at random; sometimes each univalent split and the halves went to opposite poles; and sometimes some of the univalents went as halves to opposite poles, while the halves of the rest failed to disjoin and went together to one or the other pole. In still other cells the entire chromosome group cohered in an irregular mass in the center of the cell. Micronuclei occurred frequently, as a result of chromosomes failing to be included in the telophase nuclei. The second division was observed to proceed more or less regularly if the chromosomes went to the poles as wholes at first anaphase, although supernumerary micronuclei frequently occurred. The behavior at second division was not determined for cells where all the univalents split at the first division nor where restitution nuclei were formed.

Origin of reciprocal translocations

KIHARA and NISHIYAMA (1937), KOSTOFF (1937), and HOWARD (1938) have pointed out that pairing between partially homologous chromosomes in hybrids may lead to the occurrence of segmental-interchange rings in the progeny of the hybrids. This explanation could apply also to haploids of *T. vulgare*, where a small amount of pairing occurs. GAINES and AASE (1926) reported occasionally one and rarely more pairs in their haploid, and RAW (1937) observed 0–5 bivalents and an occasional trivalent in *T. vulgare* haploids. Crossing over between a pair of non-homologous or partially homologous chromosomes (figure 10) would constitute a reciprocal translocation, and would result in a ring of four in backcrossed progeny if the two interchanged chromosomes were included in the same gamete. The formation of a single restitution nucleus such as was sometimes observed by GAINES and AASE at the end of the first division would permit both interchanged chromosomes to go to the same gamete. Or, if all the univalent chromosomes split and disjoined at the first division, the two chromosomes which were paired might disjoin tardily and both be included in the same telophase nucleus.

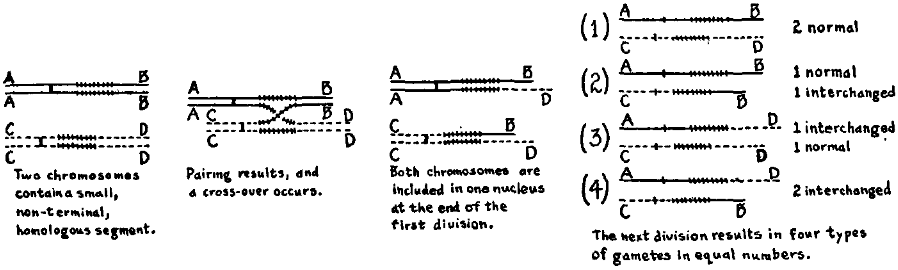

FIGURE 10.—Probable method of origin of reciprocal translocations from a haploid of *Triticum vulgare*. A gamete of type 4, if fertilized by a normal germ cell, will produce a plant with a ring of four at meiosis, while types 2 and 3 will give a plant with a chain of four.

As emphasized by HOWARD (1938) and illustrated in figure 10, through random segregation of the four chromatids of a bivalent in which crossing over had occurred, only one-fourth of the gametes formed from spore-mother cells in which an interchange had taken place would have two interchanged chromosomes, one-fourth would be normal, and one-half would contain one normal and one interchanged chromosome. An egg of this last type would have a duplication and a deficiency, and if fertilized by a normal sperm, would produce a plant with a chain of four, as in figure 9. The fact that no such plant was discovered in the immediate progeny of the haploid may have been due to the difficulty of detecting the infrequent chains of four and trivalents which would have occurred if the deficient-duplicated segment was small.

Origin of monosomes and trisomes

These two abnormalities will be discussed together because every mode of origin to be suggested for one also applies to the other. Where only

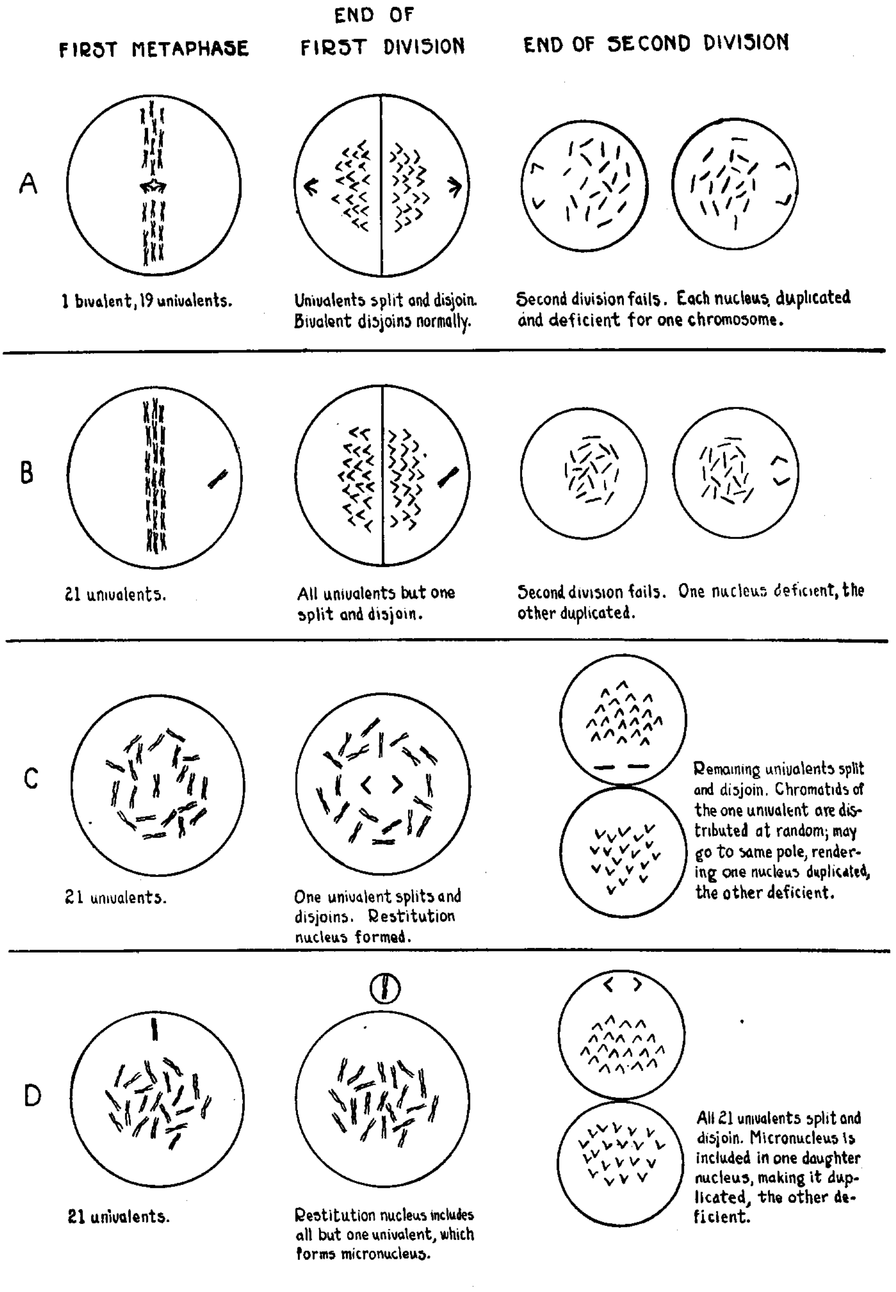

FIGURE 11.—Possible methods of origin of deficient and duplicated gametes from a haploid of *Triticum vulgare*.

monosomes occurred, as in plants 1 to 5 and in plant 7, it is possible that these arose through random segregation of 19 or 20 chromosomes to one pole at the first division in the haploid, a possibility which does not provide for the occurrence of trisomes. However, the chance of such an unequal distribution as 20:1 is so small that its occurrence even once among so few flowers as were pollinated would be highly improbable.

One way in which monosomes and trisomes could originate has already been suggested by VON BERG (1935), as a result of his observations on meiosis in a 21-chromosome generic hybrid, *T. turgidum*×*Haynaldia villosa*. He found, as had GAINES and AASE in their wheat haploid, that frequently all the univalents split and disjoined at the first division, and he observed that at the second division, restitution nuclei were formed which included all 21 chromatids. He pointed out (figure 11, A) that the presence and normal disjunction of a bivalent in a cell where all the univalents split and go to opposite poles at the first division would render the resulting gametes deficient for one member of the bivalent and duplicated for the other member. It should be pointed out that if an interchange occurred between the two paired chromosomes, the deficiency and duplication would be equal only to the non-interchanged parts of the chromatids, and a gamete with such a deficiency-duplication for a part of a chromosome, when fertilized by a normal germ cell, would produce a plant with a chromosome constitution like that in figure 9. Pairing in such a plant would depend on the size of the interchanged segments, and might never involve a chain of four if the segments were small.

Another possible explanation of the origin of monosomes and trisomes (figure 11, B) is based on the observation of GAINES and AASE that both halves of one or more univalents sometimes fail to disjoin at the first division and are distributed together to one or the other pole, while the other univalents split and go to opposite poles. A daughter nucleus which received both halves of a univalent would be disomic for that chromosome, and the other nucleus would be nullosomic.

Another type of division in the *T. compactum* haploid of GAINES and AASE which suggests the origin of monosomes and trisomes is the inclusion of all the chromosomes in a single, restitution nucleus following failure of the first division. If one of the univalents were already divided when the restitution nucleus was formed (figure 11, C), the two chromatids might be distributed independently at the next division (which presumably would be equational for the rest of the univalents) and frequently pass to the same daughter nucleus, making that nucleus duplicated and the other deficient.

A fourth method of origin (figure 11, D) was suggested by KIHARA and NISHIYAMA (1937) for disomic and nullosomic gametes produced by the

21-chromosome hybrid *T. polonicum*×*Haynaldia villosa.* Cytological observation showed that about 30 percent of pollen mother cells formed restitution nuclei at the end of the first division and that over a fourth of these restitution nuclei were accompanied by one or more micronuclei. Each micronucleus contained a single chromosome, and this chromosome presumably divided within its nucleus at the second division. The inclusion of a micronucleus in one of the telophase chromosome groups of the dividing restitution nucleus was suggested as an explanation for disomic gametes, while the omission of micronuclei explained the origin of deficient gametes.

Finally, there must be mentioned the possibility of an interchange occurring (as in figure 10) which was large enough that a gamete of type 2 or 3 (containing only one interchanged chromatid), upon fertilization by a normal gamete, would produce a plant in which a trivalent and a univalent were regularly formed, with never a chain of four. It is doubtful, however, that such a large interchange occurs other than very rarely. Most of the chromosomes of *T. vulgare* have median or near-median centromeres, so that interchanges on both sides of the centromere, each involving the same chromatid, would be necessary to make a chromatid much more than half interchanged. From the observable looseness of the association at metaphase in wheat haploids, it is unlikely that interchanges often occur on both sides of the centromere.

DISCUSSION

Several possibilities present themselves for the use of chromosome aberrants in a broad genetic analysis of *T. vulgare.* One possible study is of the immediate effects on the plant of deficiencies and duplications of chromosomes and parts of chromosomes. Another line of attack is to use monosomes and trisomes to locate on specific chromosomes the genes of common wheat.

Hybrids of the various aberrants with wheats of the emmer group will show at meiosis whether any of the chromosomes concerned are homologous with emmer chromosomes. As previously noted, five monosomes have thus far proved to have a homolog in the emmer complement. The hybrids which involve these monosomes can presumably be used to introduce, through backcrossing, single, intact emmer chromosomes into *T. vulgare.* Observation of the effects of these emmer chromosomes may shed light on the phylogeny of *T. vulgare,* and will have obvious practical applications. By backcrossing these same hybrids to the emmer parent, it should be possible to obtain monosomics in emmer, if they are viable, and to compare the effects of the deficiencies there with their effect in *T. vulgare,* where an additional set of seven chromosomes is present.

Homologies among the 21 chromosomes of *T. vulgare* are indicated by the formation of bivalents in the haploid. Little is known about these homologies. They may consist of duplicated segments scattered among all 21 chromosomes, or they may be duplications confined to a few chromosomes. Up to five meiotic pairs have been observed in a haploid, but there is no knowledge whether these five represent the total amount of homology, or whether they are merely the random result of homologies which involve more than ten chromosomes but which are too slight ever to result in more than five pairs in a single cell. Reciprocal translocations obtained from haploids of *T. vulgare,* if due to crossing over between homologous regions, furnish a means of determining the homology of definite chromosomes and regions. If association in the haploid is restricted to certain, partially homologous chromosomes, then the translocations which result should always involve the same chromosome combinations. These could be identified by crosses among a number of plants containing translocations of different origin, and by crosses with specific nullosomics or monosomics.

It is possible that many other supposedly polyploid plants will prove amenable to the same sort of analysis as that under way on *T. vulgare.* The results of STADLER (1931), KATAYAMA (1934), YEFEIKIN and VASILYEV (1936), GERASSIMOWA (1936), and IVANOV (1938), indicate that X-rays may be effective in inducing haploidy, and SINGLETON (1938) noted the occurrence of several haploids after ultra-violet treatment of maize pollen. Twin seedlings constitute another source of haploids (NAMIKAWA and KAWAKAMI 1934; HARLAND 1936; KIHARA 1936; YAMAMOTO 1936; MÜNTZING 1937, 1938; WEBBER 1938; KASPARYAN 1938). Whether haploids of other polyploid species than *T. vulgare* will give rise to the same types of chromosome aberrations remains to be seen.

Hybrids with little chromosome pairing might be studied with profit in the foregoing fashion. If an amphidiploid could be produced and backcrossed successfully to the hybrid, the resulting plants might then contain segmental-interchange associations and whole-chromosome deficiencies and duplications.

ACKNOWLEDGMENTS

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SUMMARY

1. From a haploid of *Triticum vulgare,* 13 viable seeds were obtained by application of pollen from diploids.

2. Eleven of the resulting plants showed abnormal meiotic associations.

A total of 16 univalents, five trivalents, and two rings of four were present in the 11 individuals, the most aberrant of which had two univalents, two trivalents, and a ring of four.

3. Nearly all of the aberrant plants differed from normal in morphology, color, size, or vigor. Selfed seeds were obtained on all but one, and that one was fertile to pollen from a normal plant.

4. Nullosomic plants were obtained in the progeny of two monosomics. One of these was dwarfed and sterile, while the other was only semi-dwarf and was fertile.

5. Crosses of *T. durum* with eight monosomic plants of different origin showed that five of the eight involved a chromosome homologous to one of those of *T. durum.*

6. A tetrasomic plant, phenotypically indistinguishable from normal, was found in the progeny of a trisomic.

7. Rings of four were presumably the result of segmental interchanges which occurred in the haploid as crossovers between paired, partially homologous chromosomes.

8. From a plant with a ring of four, an individual with an unstable chain of four was obtained, supposedly as a result of the functioning of a deficiency-duplication gamete.

9. The various chromosome aberrations apparently resulted from some regulatory process in the haploid which favored the production of spores with near the somatic number of chromosomes. The use of these aberrations provides a new method for the genetic anlysis of *T. vulgare*—a method which may be applicable to polyploid plants in other genera.

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