STERILITY IN WHEAT HYBRIDS. II. CHROMOSOME BEHAVIOR IN PARTIALLY STERILE HYBRIDS

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TABLE OF CONTENTS

INTRODUCTION

The cultivated species of wheat can be divided into three definite groups according to their sterility relationships in interspecific crosses (SAX 1921). The Einkorn group contains only one species, *Triticum monococcum;* the Emmer group consists of *T. dicoccum*, *T. durum*, *T. turgidum*, and *T. polonicum;* the Vulgare group consists of *T. Spelta*, *T. vulgare*, and *T. compactum*. Einkorn crossed with members of the Emmer group or with members of the Vulgare group results in F_1 hybrids which are almost if not quite sterile. Species of the Emmer group crossed with species of the Vulgare group result in partially sterile F_1 hybrids. The species

within each group are inter-fertile. These sterility relationships are in accord with the recent taxonomic classifications (TSCHERMAK 1914, PERCIVAL 1921), with serological relationships as determined by ZADE (1914), and with VAVILOV'S (1914) classification in respect to rust resistance.

In 1917 a study of the chromosomes of the wheat species and their hybrids was undertaken to determine the chromosome relationships in the cultivated species and the chromosome behavior in partially sterile hybrids. A knowledge of the chromosome behavior should be of value both in an analysis of the origin and relationships of the various species and in a genetic analysis of partially sterile hybrids. A cytological and genetic analysis of wide species crosses involving a certain amount of incompatibility, is especially important in view of EAST'S (1921) conclusions in regard to the origin of important domesticated plants and animals.

PREVIOUS CYTOLOGICAL WORK WITH WHEAT

A comparatively large number of investigators have made cytological studies of the chromosome number in wheat. OVERTON (1893), KÖRNICKE (1896), DUDLEY (1908), NAKAO (1911), BALLY (1912, 1919) and PERCIVAL (1921) all report 8 as the haploid chromosome number in *T. vulgare*. SPILLMAN (1912) reports about 6 chromosomes in rye and about 40 in wheat. In all of these cases the papers are very poorly illustrated or are not illustrated at all. PERCIVAL and SPILLMAN present no drawings or figures to support their conclusions. In the other papers the drawings are not convincing, and if they faithfully represent the preparations the material was undoubtedly poorly fixed. The chromosomes are pictured as more or less shapeless masses and lack detailed shape and structure. Such an appearance is often due to poor fixation.

In 1917 the writer (SAX 1918) found about 28 chromosomes in the first division of the fertilized egg cell in *T. durum*. At about the same time SAKAMURA (1918) reported the following chromosome counts in wheat: *T. monococcum*, 14 (diploid); *T. durum*, *T. polonicum*, *T. turgidum* and *T. dicoccum*, 28; and *T. Spelta*, *T. vulgare* and *T. compactum*, 42. SAKAMURA'S counts were made almost exclusively from preparations of root tips. The paper contains no illustrations of any kind.

The behavior of the chromosomes in partially sterile wheat hybrids has been described by KIHARA (1919). The hybrids used were *T. durum* × *T. vulgare*, *T. turgidum* × *T. compactum*, and *T. polonicum* × *T. Spelta*. The chromosome numbers of the parents were not determined, but were based on the work of SAKAMURA (1918). The F_1 hybrids were found to

have 35 diploid chromosomes, the sum of the gametic number of the parents. The behavior of the F_1 chromosomes in the reduction divisions is described as follows. At the time of the heterotypic division 14 bivalent and 7 univalent chromosomes are formed. The double chromosomes become oriented on the equatorial plate, but some of the single chromosomes may lie outside of the equatorial plate. As the double chromosomes divide normally and pass back to the poles, the single chromosomes become oriented on the plate, divide equationally and join the 14 chromosomes already at either pole. In the homotypic division 14 chromosomes pass to the poles leaving about 7 (often 5 or 6) chromosomes on the plate. These 7 chromosomes do not divide equationally at this time but pass apparently at random to either pole without dividing. Tetrads are usually formed normally but in some cases chromatic bodies are found in the cytoplasm of the one-nucleate microspores. Most of KIHARA'S preparations were obtained from anthers, but somatic tissue was also used for determining the chromosome number in the F_1 plants.

KIHARA (1921) has also investigated the chromosome number in the F_2, F_3 and F_4 of the above partially sterile hybrids. In 8 F_2 plants the somatic chromosome number was found to vary from 31 to 42. In 16 F_3 plants the chromosome number varied from 28 to 41, and in 2 F_4 plants the chromosome number was 39 and 42. The number of univalent chromosomes was found to vary from 0 to 5. Some correlation was found in the F_3 between chromosome number and fertility,—the plants with a chromosome number approaching 42 were more fertile than plants with 38 or 39 chromosomes. The paper is illustrated with one plate of microphotographs which, although hardly adequate to support the author's conclusions, do indicate that he had excellent preparations.

It is evident that there is considerable dissension in regard to the chromosome number in wheat. Six investigators report 8 as the haploid chromosome number, one investigator reports about 40, two investigators report 14 for *T. durum*, and one investigator finds 7, 14 and 21 according to the species used. The last investigator (SAKAMURA) does not present any illustrations to support his counts. Since the value of a cytological paper is largely dependent on the character of the illustrations used, it is not surprising that SAKAMURA'S results have been questioned (PERCIVAL 1921). In view of the different chromosome numbers reported by various investigators and the paucity of illustrations presented, a thorough cytological investigation of the chromosomes of wheat, with adequate illustrations, is justified.

MATERIAL AND METHODS

The following species of wheat were used in the present investigation:

Species	*Variety*
Triticum monococcum L.	*Hornemanni* Körn.
Cultural species	
T. durum Desf.	*hordeiforme* Körn. (Kubanka)
(*T. aestivum* L. subsp. *durum* (Desf.) Thell.)	
T. polonicum L.	*villosum* Körn. (Polish)
T. turgidum L.	*pseudo-cervinum* Körn. (Alaska)
(*T. aestivum* L. subsp. *vulgare* (Vill.) Thell. var. *turgidum* (L.) Druce)	
T. vulgare Vill.	*lutescens* Körn. (Marquis)
(*T. sativum* Lam. *T. aestivum* L. subsp. *vulgare* (Vill.) Thell.)	*erythrospermum* Körn. (Preston) *albidum* Körn. (Amby) (Bluestem)
T. compactum Host.	*Humboldtii* Körn. (Wash, Hybrid 143.)
(T. *aestivum* L. subsp. *vulgare* (Vill.) Thell. var. *compactum* (Host.) Sacc.)	
T. *Spelta* L. (*T. aestivum* L. subsp. *vulgare* (Vill.) Thell. var. *Spelta* (L.) Sacc.)	*album* Körn.

The chromosome behavior in the following F_1 hybrids was investigated.

(1) *T. monococcum* ♀ × *T. turgidum* ♂
(2) *T. compactum* ♀ × *T. durum* ♂
(3) *T. vulgare* (Amby) ♀ × *T. durum* ♂
(4) *T. durum* ♀ × *T. vulgare* (Amby) ♂
(5) *T. durum* ♀ × *T. vulgare* (Bluestem) ♂
(6) *T. vulgare* (Bluestem) ♀ × *T. durum* ♂
(7) *T. vulgare* (Bluestem) ♀ × *T. turgidum* ♂

For convenience the species of wheat may be divided into the three sterility groups, the Einkorn group, the Emmer (E) group, and the Vulgare (V) group. In measuring pollen grains several additional varieties of *T. vulgare* were used as well as *T. aegilops* Beauv.

The cytological work was started at Bussey Institution in 1917 but was interrupted until 1919 when it was resumed in Illinois. Since 1920 the work has been carried on at the Maine Agricultural Experiment Station and at the Bussey Institution.

Considerable difficulty was experienced at first in obtaining well fixed material. Often the chromosomes were found clumped together in such a way that accurate counts could not be made. SAKAMURA was unable to obtain well fixed anthers and used root tips for his preparations. Apparently none of the earlier investigators were able to get good fixation of wheat chromosomes at the time of the reduction divisions, if we may judge from the appearance of the illustrations. Poor fixation results in a grouping of the chromosomes into a varying number of shapeless masses of chromatin. I have frequently found approximately 8 such masses in poorly fixed material. In well fixed pollen mother cells the chromosomes are clearly defined, there is little shrinkage, and the cytoplasm shows great detail of structure.

The usual fixatives,—chrom-acetic acid, and Flemming's solution, gave good results in some cases, but the best results were obtained with a modified Bouin's solution developed by ALLEN (1916). This fixative has been used successfully in MCCLUNG's laboratory when chromosome counts were desired. The modified Bouin's solution apparently prevents the clumping of the chromosomes and thus facilitates a detailed examination of the individual chromosomes.

In some cases the entire wheat head was fixed when it was about an inch long, but much better results were obtained when the anthers were dissected out. The best fixation was found where the fixative had to penetrate only a thin layer of tissue.

Sections were cut 10–12μ thick and were stained with Haidenhain's iron-haematoxylin. The drawings were done in ink and in all cases were made from single sections. I am greatly indebted to my wife for much assistance with the drawings, to Professor I. W. BAILEY for doing most of the work in preparing the photographs, and to Doctor EAST for valuable suggestions.

THE CHROMOSOMES IN THE CULTIVATED SPECIES OF WHEAT

The chromosomes in the cultivated species of wheat will be considered in order of their sterility and taxonomic relationships.

In Einkorn, *T. monococcum*, there are clearly 7 pairs of chromosomes in the pollen mother cells. At the time of diakinesis the paired chromosomes can be seen twisted about one another (figure 1). Often delicate fibers can be seen between the two members of a bivalent chromosome and between pairs of chromosomes. The bivalent chromosomes shorten, the nuclear membrane disappears, and the chromosomes become oriented on the equatorial plate. A polar view of the chromosomes at this stage is

shown in figure 2. In the heterotypic division the spindle fibers have a subterminal attachment to the chromosomes. The division proceeds regularly and there are no lagging chromosomes (figures 3, 4 and 38, plates 1 and 3). Occasionally a bivalent chromosome is drawn out into a long thread during division, as if the two members of the pair were firmly united at one end and were separated only by considerable tension. As the chromosomes pass back to the poles they become distinctly two-parted (figures 4 and 5). At this stage, the late anaphase, the chromosomes can be most readily counted. The numbers of chromosomes are clearly shown in the polar views of the late anaphase by figures 5 and 37. In the telophase the chromosomes lose their identity as individuals and then pass into the resting stage.

The chromosomes of the second or homoeotypic division are long, much like somatic chromosomes, and are difficult to count. The second division is normal and there are no lagging chromosomes (figure 6). This division takes place at right angles to the heterotypic division and in the same plane so that the resulting microspores of each tetrad are in one plane.

In the species of the Emmer group,—*T. durum*, *T. turgidum*, *T. polonicum* and *T. dicoccum*,—there are 14 gametic chromosomes. In *T. durum* and *T. polonicum* the number has been determined in the pollen mother cells, but in other species of this group the number was determined only approximately from somatic counts.

The 14 pairs of chromosomes in the diakinesis of *T. durum* are shown in figure 7. In most cases the double nature of the bivalents is clearly evident. Often some pairs appear to be longer than others but such differences may be due partly to different stages of contraction. The chromosomes on the equatorial plate are shown in figures 8 (*T. polonicum*) and 9 (*T. durum*) and the anaphase is shown in figure 39. When well fixed the chromosomes can be easily counted at these stages. A side view of the metaphase of the heterotypic division is shown in figure 10. The division is regular and there are no lagging chromosomes at any time (figure 11). The two-parted chromosomes on reaching the poles pass into the resting condition and a cell plate is formed (figure 12). The second division is normal and the four cells of the tetrad are formed in one plane (figure 13).

There are 21 haploid chromosomes in the species of the Vulgare group. The chromosomes in the diakinesis are often grouped around the nucleolus, and owing to the relatively large number it is not easy to count them at this stage. Accurate counts can be obtained from the metaphase of the heterotypic division. A polar view of the metaphase of *T. Spelta* is shown

in figure 14 and a similar view of the chromosomes of *T. vulgare* is shown in figures 15 and 40. The subterminal attachment of the spindle fibers together with the anastomosis of certain parts of the bivalent chromosomes results in unusual distortion of the chromosomes at the time of division (figure 16). The free ends of the chromosomes are usually short and thick, while the portions between the fiber attachment and the united ends are often drawn out into thin threads. There are no lagging chromosomes at any time either in the anaphase or telophase (figures 17, 19 and 44). The chromosomes in the late anaphase can be easily counted (figure 18). The chromosomes in the second division are very long and can be counted only with difficulty. The approximate number may be counted in figure 20, which is the metaphase of the second division in *T. vulgare*. The division is normal and the tetrads are formed as in the other groups of species.

There is apparently little difference in the size of the individual chromosomes within or between species. Often several long bivalents can be seen in diakinesis in the Emmer and Vulgare groups, but the number of these varies even in the same individual plant. In the side views of the metaphase certain chromosomes are longer than others, but here again the number of very long chromosomes varies and it is probable that the longer chromosomes have no greater volume than some of the shorter ones. In the figures it appears that the individual chromosomes of Einkorn are larger than the chromosomes of the other species, but such an appearance may be entirely due to differences in fixation and staining. The preparations of Einkorn were stained much more deeply than preparations of the other species.

In general there is some correlation between chromosome number and cell size, as indicated by the size of the pollen mother cells in the different species. Often, however, the cells are cut in such a way that a cross section does not indicate their relative volume. Differences in stages of development as well as differences in fixation may also cause differences in apparent size of cells even in the same species.

The chromosomes of rye have never been pictured, so several figures of rye are presented in figures 41A and 41B. The twisted pairs of chromosomes in diakinesis is especially well shown in figure 41A. In several cases all 7 chromosomes can be counted even at the stage of diakinesis.

THE CHROMOSOMES IN STERILE AND PARTIALLY STERILE SPECIES HYBRIDS

T. monococcum × *T. turgidum*

In the cross of Einkorn × Alaska the F_1 plant has 21 somatic chromosomes, 7 contributed by the Einkorn parent and 14 contributed by the Alaska parent. At the time of the first reduction division about seven pairs of chromosomes are formed, leaving approximately 7 single chromosomes. Presumably the 7 Einkorn chromosomes pair with 7 of the Alaska chromosomes, leaving 7 single or univalent chromosomes contributed by the Alaska parent. The bivalent chromosomes orient themselves on the equatorial plate, but the single chromosomes are usually found at or near the poles of the spindle figure,—seldom on the equatorial plate. In figure 22 there are 6 pairs of chromosomes shown on the heterotypic plate and one pair which has divided. Four single chromosomes lie at one pole and three at the other, a total of 7 single chromosomes. The number of single chromosomes at the poles varies somewhat, but the total number is approximately 7 in most cases (table 1).

TABLE 1

Assortment of single chromosomes in the heterotypic division of the F_1 Einkorn × Alaska.

Number of single chromosomes at either pole	4 3	4 4	5 3	4 2	5 2	6 1	5 4	3 2	6 3	5 6
Total singles	7	8	8	6	7	7	9	5	9	11
Actual frequency	8	4	4	3	3	3	2	1	1	1
Theoretical frequency	17				10	3				

The number of single chromosomes may vary due to segmentation, or they may lie on the plate with the double chromosomes in some cases. It is also possible that less than 7 bivalent chromosomes are formed, in which case the total number of singles would be 9 or 11. In general, however, the chromosome number is approximately 7 and the distribution of about equal numbers of single chromosomes to either pole occurs with greatest frequency as expected.

The single chromosomes remain at the poles while the bivalent chromosomes divide and join the single chromosomes. The total number of chromosomes at either pole is then usually about 10 or 11 (fig. 23). As the members of the bivalent chromosomes pass to the pole they split

longitudinally as usual (figure 24). All chromosomes both single and double are grouped together in the telophase (figure 25).

In the homoeotypic division approximately ten chromosomes are found at the metaphase (figure 27). These chromosomes are long and curved. They consist of the 7 divided bivalents plus 0 to 7, but usually 2 to 5, univalent chromosomes. Since the univalents did not divide during the heterotypic division they would be expected to divide normally in the homoeotypic division. The actual behavior of the chromosomes during the second division is difficult to determine owing to the length of the chromosomes and the paucity of critical stages. The division appears to be normal, however, and seldom were any lagging chromosomes found (figure 26). The tetrads are formed as in the case of the parental species and in comparatively few cases are chromatin granules found outside of the nuclei. The tetrads separate into one-nucleate pollen grains which appear to be normal. Very few of the one-nucleate pollen grains develop normally, however, and only about 2 to 3 percent of the mature pollen grains appear normal. Probably none of them is functional.

In a few cases the univalents were found on the heterotypic plate after the bivalents had divided, indicating that the behavior of the univalents in the reduction division may vary in different individuals.

Emmer group × *Vulgare group*

In crosses between members of the Emmer group and members of the Vulgare group the sum of the gametic numbers of chromosomes is 35. Such F_1 plants will have 14 chromosomes contributed by one parent and 21 chromosomes contributed by the other parent. In the pairing of the chromosomes for reduction the 14 chromosomes of the Emmer group presumably pair with 14 chromosomes of the Vulgare group, leaving 7 univalent Vulgare chromosomes. At any rate in diakinesis there are about 14 bivalents and 7 univalents. The bivalent and univalent chromosomes can easily be distinguished in the metaphase of the heterotypic division. A polar view of the metaphase of the F_1 of Amby (V) × Kubanka (E) is shown in figures 28 and 42. The 7 univalent chromosomes are long, slender and V-shaped, while the bivalent chromosomes are like the bivalents in the normal heterotypic division in the parent species. A similar stage is shown in the F_1 of Bluestem (V) × Alaska (E) in figure 29. The univalents are usually arranged on one side of or around the group of bivalents.

Some of the single chromosomes often lie outside of the equatorial plate and appear to be distributed more or less at random in the division figure (figure 30). Usually only two or three single chromosomes can be seen outside of the equatorial plate in a side view, but in a polar view all of the univalents may lie outside of the group of bivalents. As the bivalents divide and pass to the poles the univalent chromosomes become oriented on the equatorial plate (figures 31-34, 43 and 45). The univalents may vary in number due possibly to the failure of all 14 chromosomes to pair, or to the premature or accidental passage of single chromosomes to the poles (figure 30).

TABLE 2

Number of lagging single chromosomes in the heterotypic division of F_1 of Emmer group × Vulgare group.

Number of lagging chromosomes	4	5	6	7	8	9
Frequency	1	3	7	22	2	1

Table 2 was prepared from well fixed division figures before all of the univalents had separated and where the figure was apparently intact. In the majority of cases 7 lagging univalents were found (figures 32 and 34). In one case 9 single chromosomes appeared to be present (figure 31), but at least one univalent may be segmented into two parts. The univalents are frequently somewhat constricted in the centers where the spindle fibers are attached. The grouping of the bivalents on one side of the spindle is often found (figure 33). The 14 chromosomes at the poles, resulting from division of the bivalents, can frequently be counted with little difficulty, but it is difficult to picture them because they are so compactly grouped.

The segmented univalent chromosomes divide and pass to the poles (figure 35). In most, if not in all cases, there are no chromosomes left free in the cytoplasm, but all are grouped together in the telophase (figures 36 and 46). The daughter nuclei thus formed pass into the resting stage.

In the second division some univalent chromosomes are found outside of the equatorial plate in the metaphase (figure 47). In the late anaphase or telophase univalent chromosomes are found lagging after most of the chromosomes have reached the poles (figures 37 and 48). The number of lagging chromosomes varies, with the mode at 5. Perhaps some of the chromosomes at the poles in the metaphase (figure 47) remain there

and fail to take their place on the plate, or single chromosomes may accidentally pass to the poles with the original members of the bivalents. The following table shows the distribution of the single lagging chromosomes in the second division.

TABLE 3

Number of lagging chromosomes in the homoeotypic division. Vulgare group × Emmer group.

Number of lagging chromosomes	2	3	4	5	6	7
Frequency	1	3	5	10	5	2

The lagging chromosomes do not divide equationally but pass apparently at random to either pole. Thus the four microspores each contain 14 chromosomes presumably contributed by both parents according to chance and from 0 to 7 additional chromosomes of the Vulgare parent, the latter number also depending on chance distribution. The fact that the univalent chromosomes divide but once, equationally of course, while the bivalents divide twice in the course of gametogenesis, is in accord with the usual conception of the nature of the reduction divisions.

In some cases the lagging chromosomes fail to go back to the poles and several chromosomes may lie outside of the reconstructed nucleus, usually in the vicinity of the newly formed cell wall. As a rule, however, microspores are formed which have no chromatic material in the cytoplasm outside of the nucleus. These one-nucleate pollen grains appear to be entirely normal so far as the morphological structure is concerned. In many cases, however, they are unable to develop into normal pollen grains. About 20 percent of the pollen of the F_1 plants resulting from Emmer group × Vulgare group crosses is obviously imperfect as indicated by smaller size and meager contents. Undoubtedly a larger percentage is not functional because of physiological or other imperfections in pollen grains that appear morphologically perfect.

THE POLLEN GRAINS IN PARENTS AND F_1 HYBRIDS

There is a striking correlation between chromosome number and the size of the pollen grains in the wheat species studied. Such a relation would be expected if BOVERI'S conclusions concerning chromosome number and cell size have a general application. The pollen grains are especially good for testing such relationships because they consist of only several cells, their volumes are easily determined, and they can be meas-

TABLE 4

Size and variability of pollen grains of wheat varieties and species and of some F_1 hybrids. 1921 data.

VARIETY OR F_1 HYBRID		DIAMETER IN MICRONS (CLASS CENTERS) 37.5	39.0	40.5	42.0	43.5	45.0	46.5	48.0	49.5	51.0	52.5	54.0	55.0	57.0	58.5	60.0	61.5	63.0	64.5	66.0	67.5	N	MEAN	σ	C. V.	VOLUME CU. μ
Aegilops ovata	W	1	8	15	15	16	5	2	1														63	43.55±.18	2.12±.13	4.87±.29	53,000
	L							1	3	5	19	20	9	5	1								63	53.55±.15	1.80±.11	3.35±.20	
Einkorn		3	12	23	33	44	13	6	4														138	44.02±.13	2.19±.09	4.98±.20	45,000
Kubanka	E						1	3	13	19	20	22	10	4	3	1							96	51.22±.18	2.62±.13	5.12±.24	70,000
Alaska	E						2	4	8	13	14	23	22	7	1	1							95	51.76±.19	2.68±.13	5.18±.25	73,000
Polish	E					1	5	6	19	17	27	31	5	1	1								113	50.34±.16	2.47±.11	4.90±.22	67,000
Emmer	E						2	2	8	19	29	26	11	9	4	2							112	51.70±.17	2.62±.12	5.07±.23	72,000
Spelt	V								2	2	4	13	15	17	11	12	8	3		1			88	55.59±.23	3.15±.16	5.67±.28	90,000
Marquis	V									2	5	18	20	27	18	5	4						99	54.91±.15	2.27±.11	4.14±.20	87,000
Amby	V									1	5	14	16	26	15	8	4	2					91	55.30±.17	2.47±.12	4.46±.22	89,000
Preston	V									2	4	21	23	25	20	5	5						105	54.92±.15	2.29±.11	4.17±.19	87,000
Royalton White	V									1	5	15	24	33	14	7	2						101	54.92±.14	2.06±.10	3.75±.14	87,000
Kota V × Royalton	V							1	1	3	7	12	17	21	18	8	4		1				93	54.95±.20	2.85±.14	5.19±.25	87,000
Spelt V × Marquis	V			1	1	1	2	1	6	4	8	9	12	18	17	13	16	5	4	1			119	55.37±.29	4.67±.20	8.44±.37	89,000
Polish E × Emmer	E				1	3	2	7	8	10	13	18	15	12	9	1	1		1				101	51.94±.26	3.85±.19	7.40±.35	73,000
Emmer E × Polish	E			1	1	2	2	4	9	9	9	24	12	10	10	5	3	2	2				105	52.73±.29	4.37±.20	8.28±.39	77,000
Kubanka E×Marquis	V	1	2	3	4	8	8	4	4	3	7	15	10	6	7	11	12	6	4	4	1		120	53.04±.43	6.39±.30	13.07±.58	78,000

ured at the same stage of development. The size and variability of the pollen grains of most of the wheat species and of F_1 hybrids between varieties, compatible species, and members of different sterility groups are shown in table 4.

In *T. aegilops ovata* the pollen grains were not spherical and two dimensions were taken to determine the volume. In all other cases the pollen grains were approximately spherical, so only the diameter was measured. In all cases only the apparently good pollen grains were used. Only in the partially sterile hybrid Kubanka × Marquis, was the percentage of obviously poor pollen grains more than 1 to 2 percent. The pollen grains were mounted in lactic acid and were measured with an ocular micrometer.

In Einkorn with 7 chromosomes the mean volume of the pollen grains, measured in thousands of cubic microns, is 45. In the species of the Emmer group with 14 chromosomes the mean volume of the pollen grains is about 70. In the species of the Vulgare group the mean volume of the pollen grains is about 88. The F_1 hybrids resulting from crossing members of the Vulgare group, have pollen grains of about the same size as the parents, and a similar condition obtains for F_1 hybrids within the Emmer group.

Not only is there a consistent and significant relation between pollen-grain size and chromosome number in the various species groups, but there is also a consistent relation between heterozygosis and pollen-grain variability. In the homozygous parents the coefficient of variability for pollen-grain diameter ranges from $3.75 \pm .14$ to $5.67 \pm .28$. In the cross, Kota × Royalton White, both parents belong to the same species, *T. vulgare*, and the pollen-grain variability is little if any greater than for the parents. In the cross, Spelt × Marquis, the parents belong to different species, but to the same sterility group, and the pollen of the F_1 is significantly more variable than for the parents or the preceding varietal cross. The reciprocal crosses between Polish and Emmer also involve different species, but only one sterility group, and the pollen-grain variability in the F_1 is significantly greater than in the parents. The F_1 resulting from Kubanka × Marquis has pollen grains almost three times as variable as the parent species. In this case the parents belong to different sterility groups and the F_1 is partially sterile. The striking increase in pollen-grain variability is not due to obviously aborted pollen grains because only the apparently good pollen grains were measured It will be noted that the distribution is not especially skew or bimodal as

would be the case if the increased variability were due only to poorly developed or aborted pollen.

Apparently environmental conditions may cause differences in pollen-grain size. The size of the pollen grains in 1920, measured in thousands of cubic microns, was 72 for Einkorn, 94 for the Emmer group and 114 for the Vulgare group. The relative sizes of the pollen grains of the three sterility groups was about the same in 1920 and 1921.

Pollen-grain size and chromosome number are also correlated in a similar manner in the species of oats.

DISCUSSION

Polyploidy in plant species

The occurrence of the gametic chromosomes in multiples of 7 in the species of wheat suggests that the Emmer and the Vulgare groups are tetraploid and hexaploid forms, respectively, of an original type with 7 chromosomes. The origin of new species by tetraploidy in other genera would tend to support such a view. *Oenothera gigas*, a mutant from *Oe. Lamarckiana*, is the best known case of tetraploidy in plants. The chromosome number of the mutant was found to be 28 as compared with 14 for the parental species (LUTZ 1907). Miss DIGBY (1912) found a tetraploid form of *Primula kewensis* with 36 somatic chromosomes. Tetraploidy has been found recently in Datura (BLAKESLEE, BELLING AND FARNHAM 1920). In all of the above cases tetraploidy has occurred while the species were under observation. The hereditary behavior of the tetraploid plants shows a doubling of genetic factors and thus supports the cytological observations.

Chromosome duplication has also been found in other species which have not been under such close observation and which have not been tested by breeding experiments. In Hieracium there are species with 18, 27, 36 and 42 somatic chromosomes (ROSENBERG 1917). In Crepis species are found with 6, 8, 10, 16, 18, 24 and 42 somatic chromosomes. ROSENBERG (1920) believes that the species with the higher chromosome numbers are caused by the duplication of one or more pairs of the chromosomes in the primary species, *C. virens*, with 3 pairs of chromosomes. In the species with 8 chromosomes the medium-sized pair of chromosomes is reduplicated while in the "*gigas*-mutant," *C. Reuteriana*, each pair is reduplicated. In the genus Rosa species are found with 14, 21, 28, 35 and 42 somatic chromosomes (TÄCKHOLM 1920).

In Chrysanthemum TAHARA (1915) finds in different species haploid numbers of 9, 18, 27, 36 and 45. GATES (1913) lists a number of other cases of tetraploidy in plant and animal species and additional cases have been found in the past few years.

Genetic behavior of polyploid species

In tetraploid plants the doubling of the chromosome number results in a duplication of the genetic factors. Thus tetraploidy can be detected not only by chromosome counts but also by the genetic behavior of hybrids of tetraploid races. If the reduplicated chromosomes of a tetraploid or hexaploid species, or to use BLAKESLEE'S (1920) terminology, the members of the tetrasomic and hexasomic sets, assort in pairs, the usual 15 : 1 or 63 : 1 ratios will result in F_2. If, however, the chromosomes of a tetrasomic or hexasomic set assort at random in an F_1 hybrid a 35 : 1 or 399 : 1 ratio will be found in the F_2. Furthermore, in such tetraploid and hexaploid plants the number of recessive factors may often exceed the number of dominant factors in heterozygous individuals in F_2 hybrids. There is evidence that in some cases either allelomorph of a pair of characters may be dominant if an excess of factors of one character are present. In the case of starchy and corneous endosperm in maize, HAYES and EAST (1915) have found that the character borne by the mother plant was always dominant, due presumably to the dominance of the two factors contributed by the mother, as a result of polar fusion, over the single factor contributed by the male parent. In Drosophila it has been found that the two recessive genes for vermilion and sable dominate the normal allelomorphs. When the mutant and normal factors are in equal numbers the normal is dominant (MORGAN 1919). Sex in Drosophila is determined by the ratio of X chromosomes to autosomes. BRIDGES (1921) has found that the ratio of 2 X : 2 sets of autosomes produces a female while 1 X : 2 sets of autosomes produces a male and the ratio 2 X : 3 sets of autosomes produces an intermediate condition, the intersex. There is also evidence that characters other than sex are also influenced by chromosome ratios.

It is possible that an excess of recessive factors may be dominant over the normally dominant factors in many cases, but because such cases become evident in diploid species only in endosperm characters, or in case of non-disjunction or other unusual chromosome behavior, they are seldom detected. The dominance of the normally recessive character would never occur in diploid plants except in endosperm characters, but in triploid, tetraploid and hexaploid plants such a relationship of dominant

and recessive characters would be found. Although few such cases have been discovered it is a possibility to be considered. We have then two possible causes for unusual genetic ratios in polyploid plants,—random assortment of chromosomes and reversed dominance due to an excess of recessive factors. The gametic constitution and genetic ratios for various combinations of diploid, tetraploid, and hexaploid hybrids are given in table 5.

In case of random assortment of chromosomes in a tetrasomic set the F_2 ratio becomes 35 : 1 instead of 15 : 1 which is found if the chromosomes assorted in pairs. In the hexasomic set random assortment would result in an F_2 ratio of 399 : 1 and in most F_2 plant populations such a segregation would not be detected. It is also obvious that a tetraploid individual can never be homozygous for a single factor in case of random chromosome assortment and in hexaploid individuals neither one nor two factors can exist in the homozygous condition. If, then, a mutation occurs in a single chromosome of a hexasomic set in which the chromosomes assort at random the homozygous condition will be attained only when all 3 chromosomes of the set are either dominant or recessive. In a homozygous hexaploid race one- and two-factor differences will not be found with random assortment of the members of the hexasomic sets.

An examination of the hereditary behavior of tetraploid species indicates that in most cases studied the chromosomes assort at random in the tetrasomic sets. MULLER (1914) in analyzing GREGORY'S data on tetraploid Primulas concluded that where more than 2 factors are present, which are normally allelomorphic to each other, the pairing of these allelomorphs usually takes place at random. He interpreted the ratio of 4.5 : 1 in a back-cross as a 5 : 1 ratio expected, rather than a 3 : 1 ratio, and showed that the ratio of 119 : 4 in F_2 may be interpreted as a 35 : 1 ratio rather than a 15 : 1 ratio proposed by GREGORY. MULLER'S analysis of GREGORY'S data indicates that in the tetraploid Primula the chromosomes of a tetrasomic pair assort at random. In Datura the duplicated chromosomes of the Poinsettia mutant apparently assort at random according to BLAKESLEE, BELLING AND FARNHAM (1920). Unusual ratios are obtained because the Poinsettia character is not carried by the pollen to any significant extent. In *Oenothera gigas* certain races when selfed produce 1 to 2 percent *nanella* mutants and pedigrees are found approaching a 3 : 1 ratio. BLAKESLEE'S (1921) analysis of DE VRIES'S data indicates that the 1 to 2 percent *nanella* segregates are recessive in a 35 : 1 ratio, and the fact that dominants from a 3 : 1 ratio throw 3 : 1 ratios or 35 : 1 ratios supports BLAKESLEE'S

TABLE 5

Result of crossing diploid, tetraploid, and hexaploid species when (1) the allelomorphic chromosomes unite in homologous pairs, and when (2) they pair at random. The F_2 ratios, $R : r$, are given when (a) an Rrr genotype appears as an R phenotype and when (b) an Rrr genotype appears as an r phenotype.

		CHROMOSOMES UNITE IN HOMOLOGOUS PAIRS			CHROMOSOMES OF POLYSOMIC SET PAIR AT RANDOM		
Parents	F_1	F_1 gametes	(a)	(b)	F_1 gametes	(a)	(b)
$R_1R_2 \times r_1$ $R_1R_2 \quad r_1$	R_1R_2 r_1	R_1R_2-r_1-R_2-r_1R_2	15 : 1	13 : 3	R_1R_2-R_1r_1-r_1R_2-r_1-R_1-R_2	35 : 1	31 : 5
$R_1 \times r_1r_2$ $R_1 \quad r_1r_2$	R_1 r_1r_2	R_1-r_1r_2-R_1r_2-r_1	3 : 1	3 : 5	r_1r_2-r_1R_1-r_2R_1-R_1-r_1-r_2	3 : 1	13 : 23
$R_1R_2 \times r_1r_2$ $R_1R_2 \quad r_1r_2$	R_1R_2 r_1r_2	R_1R_2-R_1r_2-r_1R_2-r_1r_2	15 : 1	11 : 5	R_1R_2-R_1r_2-r_1R_2-r_1r_2-R_1r_1-r_1R_2	35 : 1	3 : 1
$R_1R_2R_3 \times r_1r_2r_3$ $R_1R_2R_3\quad r_1r_2r_3$	$R_1R_2R_3$ $r_1r_2r_3$	$R_1R_2R_3$-$r_1R_2R_3$-$R_1r_2R_3$ $R_1R_2r_3$-$r_1r_2r_3$-$R_1r_2r_3$ $r_1R_2r_3$-$r_1r_2R_3$	63 : 1	42 : 22	$R_1R_2R_3$-$r_1R_2R_3$-$R_1r_2R_3$-$R_1R_2r_3$ $r_1r_2r_3$-$R_1r_2r_3$-$r_1R_2r_3$-$r_1r_2R_3$ $R_1R_2r_2$-$r_1R_3r_3$-$r_1R_2r_2$-$R_1R_3r_3$ $R_2R_1r_1$-$r_2R_3r_3$-$r_2R_1r_1$-$R_2R_3r_3$ $R_3R_1r_1$-$r_3R_2r_2$-$r_3R_1r_1$-$R_3R_2r_2$	399 : 1	282 : 118
$R_1R_2r_3 \times r_1r_2r_3$ $R_1R_2r_3 \quad r_1r_2r_3$	$R_1R_2r_3$ $r_1r_2r_3$		15 : 1	22: 42		24 : 1	2 : 3
$R_1r_2r_3 \times r_1r_2r_3$ $R_1r_2r_3 \quad r_1r_2r_3$	$R_1r_2r_3$ $r_1r_2r_3$		3 : 1	0 : 64		3 : 1	0 : 400
$R_1R_2R_3 \times R_1r_2r_3$ $R_1R_2R_3 \quad R_1r_2r_3$	$R_1R_2R_3$ $R_1r_2r_3$		64 : 0	15 : 1		400 : 0	24 : 1
$R_1R_2R_3 \times r_1r_2$ $R_1R_2R_3 \quad r_1r_2$	$R_1R_2R_3$ r_1r_2		63 : 1	3 : 1		399 : 1	324 : 76
$R_1R_2 \times r_1r_2r_3$ $R_1R_2 \quad r_1r_2r_3$	R_1R_2 $r_1r_2r_3$		15 : 1	26 : 38		3 : 1	1 : 24

conclusions. BLAKESLEE suggests that all of the Oenothera mutants are caused either by chromosomal duplication or are due to crossovers from balanced lethals as suggested by MULLER (1918). In connection with MULLER'S hypothesis, however, it may be suggested that if we accept the telosynaptic method of reduction described in Oenothera by DAVIS (1911) and GATES (1915) and at the same time accept the mechanical chiasma-type hypothesis of crossing over, there would be little or no opportunity for crossing over to occur.

In the case of Oenothera, Primula and Datura, the tetraploid forms have originated in experimental cultures and in all cases the chromosomes of a tetrasomic set appear to assort at random. In wheat there is no evidence that random assortment of chromosomes takes place in tetrasomic and hexasomic sets. The results of NILSSON-EHLE (1909), the HOWARDS (1912) and GAINES (1917) all show ratios closely approximating 15 : 1 or 63 : 1 in wheat hybrids involving several independent similar, or possibly identical, factors for the same character. Segregates can be obtained from the F_2 of a trihybrid, which are homozygous for 1 or for 2 factors, an impossible result in case of random chromosome assortment. In the segregation of capsule form in Bursa as described by SHULL (1914) the F_2 ratio approximately 24 : 1 might suggest a random assortment of chromosomes in a hexasomic set with 4 dominant factors, but such a parental type would not exist in a homozygous condition and the behavior of the F_2 segregates proves that 2 factors are involved which assort in pairs. The fact that a character may be determined by several factors does not necessarily indicate that these factors are the result of chromosome duplication.

In both wheat and Bursa multiple factors, presumably allelomorphic and in duplicate chromosomes, do not assort at random as they do in case of tetraploid Oenotheras, Primulas and Daturas. The difference in chromosome behavior may be due to the recent origin of tetraploidy in some species as compared with wheat. It is also possible that the increased chromosome number is not due to duplication of the fundamental chromosome number, or if it is, the individual chromosomes may have changed so that they assort in pairs.

Chromosome behavior in certain partially sterile hybrids

Hybrids between diploid and tetraploid, and between tetraploid and hexaploid, wheat species are completely or partially sterile, and irregular chromosome behavior occurs in the reduction divisions. In the F_1 hybrids between Einkorn with 14 chromosomes and a member of the Emmer

group with 28 chromosomes there are 7 bivalents and 7 univalents in the heterotypic spindle. The bivalents divide normally in both meiotic divisions while the singles pass at random, without dividing, to either pole in the first division and presumably divide in the second division. In hybrids between members of the Emmer group with 14 chromosomes with members of the Vulgare group with 21 chromosomes the 14 pairs of chromosomes divide as usual in meiosis while the 7 univalents lag behind but ultimately divide equationally in the first division and pass at random, without dividing, to either pole in the homoeotypic division. A comparison of chromosome behavior and sterility in similar hybrids in other genera is of interest.

In Drosera (ROSENBERG 1909) the chromosomes of the F_1 of a cross between a species with 10 haploid chromosomes and a species with 20 chromosomes, behave like the chromosomes in the Einkorn × Alaska cross in wheat. In the reduction division 10 bivalents and 10 univalents are found. The single chromosomes lag and apparently go at random to either pole without dividing. The second reduction division is not described.

In the F_1 of *Oenothera lata* × *Oe. gigas* GATES (1909) found the chromosome number to be 20 or 21, the sum of the gametic numbers of the parents. In the reduction division 10 or 11 paired chromosomes were found on the heterotypic spindle. The division is somewhat irregular in some cases, but DAVIS (1911) has found a rather loose association of the chromosomes in the parental types. GEERTS (1911), however, found 7 bivalents and 7 univalents in the reduction division of the F_1 of *Oe. Lamarckiana* × *Oe. gigas*. The single chromosomes pass to either pole without dividing, usually 3 to one pole and 4 to the other. In the second division the univalents also divide irregularly.

The number of somatic chromosomes in species of Hieracium ranges from 18 to 42. In *H. excellens* (ROSENBERG 1917) with 42 chromosomes, 18 pairs of chromosomes are found on the heterotypic spindle in addition to 6 univalents. In the F_1 of *H. auricula* (18 chromosomes) × *H. aurantiacum* (36 somatic chromosomes), 9 bivalents were found with 8 or 9 univalents in the reduction division. The univalents divide irregularly. Similar chromosome behavior was found in other hybrids but often the number of univalents was found to vary even in the same cross.

TÄCKHOLM (1920) has found only paired chromosomes in the series 7, 14 and 21, in some Rosa species. Other species, especially those of the Canina section, have both bivalents and univalents at the time of reduction, usually 7 bivalents with 14, 21 or 28 univalents. The species which

have both bivalents and univalents in pollen reduction are thought to be hybrids which have been perpetuated for long periods of time by apomictical reproduction.

The behavior of the chromosomes in reduction divisions of species of Rosa has also been described in considerable detail by BLACKBURN and HARRISON (1921). In *R. Sabini* (*R. pimpinellifolia* × *R. sylvestris*) with 42 chromosomes, there are 14 bivalents and 14 univalents on the heterotypic spindle. The univalents lag behind in division but ultimately divide and pass to the poles. In the second reduction division the original bivalents pass rapidly to the poles and the daughter nuclei are reconstructed before the original singles reach the poles. Thus the major nuclei contain about 14 chromosomes. The univalent chromosomes form micronuclei and often a total of 8 nuclei are found which may be termed an "octad."

In one case in the above hybrid all of the chromosomes at the time of the homotypic division were on a single spindle. If development had been allowed to proceed the gametes would be able to produce a new plant octoploid in chromosome number.

In other Rosa hybrids BLACKBURN and HARRISON find a type of reduction similar to that found in *R. Sabini*, but involving 7 bivalents and 21 univalents or 14 bivalents and 21 univalents, etc. All roses showing such partial reduction are facultatively apomictical, due, according to the authors, to the stimulus of heterozygosis.

In Canna and Datura (BELLING 1921) the chromosome behavior in triploid individuals is quite different from that found in similar cases in Triticum, Rosa, Drosera, and Hieracium. In one clone of Canna the 27 chromosomes unite into 9 triads at reduction. The chromosomes of each triad pass at random, two to one pole and one to the other.

Among species hybrids in animals the chromosome behavior in F_1 reduction may vary greatly. FEDERLEY (1915) crossed two species of butterflies, each with 28 chromosomes. In the F_1 the chromosome number varied from 28 to 33 in spermatogensis, due to the varying number of single and double chromosomes on the plate. FEDERLEY believes that there is a negative correlation between the number of paired chromosomes and sterility in such cases. In another species cross FEDERLEY (1916) found little or no failure of the chromosomes to pair in reduction. In the F_1 of *Pygaera curtula* L. (29 chromosomes) with *P. anachoreta* F. (30 chromosomes) FEDERLEY (1913) found about 59 chromosomes in the reduction division, indicating that little or no pairing of chromosomes occurred. In a back-cross of the F_1 with *P. anachoreta* the chromosomes of

the same species paired leaving 29 single *curtula* chromosomes. The univalents divided equationally in both divisions, but the second division was often abnormal.

In general, triploid hybrids derived from species with different chromosome numbers have a similar type of chromosome behavior in the reduction divisions. Usually the number of bivalents is equal to the gametic number of chromosomes found in the parent with the smaller number, and the number of univalents is the difference between the chromosome numbers of the parental species. The bivalents divide normally while the univalents usually divide but once, equationally of course, and pass at random to either pole without dividing in one of the reduction divisions. Whether the single chromosomes divide in the first or second reduction division should make but little difference so far as the genetic results are concerned, providing that they divide but once. In case some or most of the univalents are not included in the functional pollen grains, as found in Rosa, the genetic behavior will be disturbed.

Chromosome behavior and sterility

The occurrence of a triploid chromosome number or the reduplication of a single chromosome is associated with more or less sterility. The relation of chromosome number and behavior to sterility is shown for Oenothera, Datura, and Triticum in table 6.

The percentage of apparently poor pollen grains as an indication of sterility is, of course, only an approximate measure, but for general purposes it is considered satisfactory. In Oenothera the species and hybrids having an additional chromosome or those which are triploid are much more sterile than the diploid or tetraploid types. Here, of course, the sterility may be disturbed also by the hybrid nature of most of the Oenotheras or due to balanced lethal factors. In Datura the reduplication of but a single chromosome results in some sterility, still greater sterility is found in the triploid individual, while the tetraploid species is as fertile as the diploid parental type. Tetraploid and hexaploid species of wheat are as fertile as diploid species. In pentaploid hybrids with 14 bivalents and 7 univalents the sterility is much less than in triploid hybrids with 7 bivalents and 7 univalents. The degree of sterility may, however, be greater than indicated by the appearance of the pollen grains. Sterility based on grains set per spikelet shows total sterility for the triploid hybrid and somewhat greater than 50 percent sterility in the pentaploid hybrid as compared with the parents. If we take into account the effect of hybrid vigor and compare the F_1 sterility

TABLE 6

Relation between chromosome number and sterility.

SPECIES	CHROMOSOME NUMBER	AVERAGE PERCENT OF POOR POLLEN
Oenothera (GATES 1915)		
Oe. gigas	28	54–72
Oe. Lamarckiana	14	42
Oe. lata rubricalyx × *rubricalyx* segregate	14	22
Oe. lata rubricalyx	14	33
Oe. semilata	15	77
Oe. lata-like	15	76
Oe. rubricalyx × *gigas*	21	81
Oe. gigas × *lata rubricalyx*	22	89
Datura (BLAKESLEE 1921)		
Normal	24	3
"New species"	48	3
Triploid	36	34
Trisomic (12 mutants)	25	8–21
Triticum (SAX 1921)		
Vulgare group	42	1
Emmer group	28	2
Einkorn group	14	1
Vulgare × Emmer F_1	35	12–22
Einkorn × Emmer F_1	21	98

with the grain set in fertile species crosses, the degree of sterility may be considered as about 60 to 70 percent in the pentaploid hybrids (see SAX 1921, table 4). The degree of sterility in pentaploid hybrids varies in different species crosses and the above is only a general statement of the facts. In Rosa there is also a high degree of correlation between chromosome duplication and sterility.

In all of the above cases the reduplication of both sets of parental chromosomes does not cause sterility or abnormal chromosome behavior. The triploid hybrid resulting from a cross of a diploid with a tetraploid species or a triploid individual resulting from other causes is characterized by abnormal chromosome behavior and sterility. In wheat, sterility is greater where the proportion of univalent to bivalent chromosomes is 1 : 1 than where the ratio is 1 : 2. In Oenothera, Datura, and in one case in Rosa sterility is associated with the reduplication of a single chromosome. The uniform relation between chromosome behavior and sterility in these cases indicates that similar factors are involved.

In some species hybrids the F_1 is completely sterile even though the parental chromosomes may be very similar. For instance *Crepis tectorum* is thought to have the same chromosome constitution as *C. virens*, but with one reduplicated pair (ROSENBERG 1919), but BABCOCK and COLLINS (1920) have found that a cross between the two species results in an F_1 individual which cannot even complete its vegetative development. Still more remarkable are the recent results of STURTEVANT (1921) with Drosophila. Seven mutant genes of *D. simulans* have been shown to be allelomorphic to mutant genes of *D. melanogaster*, but crosses of these species with a similar chromosome constitution results in sterile F_1 individuals. In other cases species with apparently similar chromosome constitution cannot even be crossed.

Sterility in wheat hybrids

A brief summary of the behavior of the F_2 generation of partially sterile hybrids will be of value in interpreting the correlation between chromosome behavior and sterility. In 1917, 84 seeds from an F_1 plant of Kubanka $\times$ Bluestem were planted in the greenhouse at BUSSEY INSTITUTION. Six seeds did not germinate; 18 germinated and grew but did not pass the rosette stage; 61 grew and formed heads, but 14 of these were completely sterile. Of the 47 plants which set grain only one or possibly 2 were as fertile as the parents. The average number of grains per spikelet for the 61 plants that headed was $.82 \pm .05$ as compared with an average of .56 for 30 F_1 plants and 2.45 for the parents. The correlation between sterility and height of the 61 plants that headed was $-.42 \pm .07$, indicating that the more sterile plants were poorly developed vegetatively.

The greater sterility of certain F_2 segregates as compared with the F_1 is shown also in a cross of *T. compactum* $\times$ *T. turgidum* grown by GAINES in 1921. The average grains per spikelet for the 293 F_2 plants that headed, was $.63 \pm .02$ as compared with $1.09 \pm .05$ grains per spikelet for the F_1. In the F_1 no plants were found in the sterility class .0—.2 grains per spikelet, while in the F_2 123 plants were in the lowest sterility class. The conditions under which the F_2 was grown were more favorable than for the F_1. Furthermore a large proportion,—probably more than half,—of the F_1 seed did not grow or did not produce plants which headed.

The relation of chromosome behavior to sterility in wheat hybrids

Let us now gather the facts that bear on the relation of chromosome behavior to sterility and to the origin and the relationships of the various

species of wheat. In general, sterility increases as the proportion of univalent chromosomes in the reduction division increases. In both triploid and pentaploid wheat hybrids the 7 univalents apparently pass at random to either pole in one of the reduction divisions. The degree of sterility may vary in pentaploid hybrids involving different parental species (HAYES, PARKER and KURTZWEIL 1920, SAX 1921). Many F_2 individuals may be less fertile than the F_1, but in the F_2 sterility is also associated to some extent with poor vegetative development. With the above cytological and genetic data it should be possible to suggest a cause of sterility in wheat hybrids.

If we assume that the tetraploid and hexaploid species are due simply to a reduplication of the chromosomes of a primary diploid species with only minor changes in the individual chromosomes, then the sterility must be due to quantitative relations between univalents and bivalents rather than any specific constitution of individual chromosomes. That such may be the case is suggested by the chromosome behavior in other genera where the univalents are known to be reduplicated chromosomes of a diploid species. With 7 univalent chromosomes assorting at random only 1 gamete in 64 would contain all or none of the univalents. If only gametes containing all or none of the univalents can develop and function, sterility would be almost complete. Such a relation of the chromosomes would explain practically all of the sterility found in triploid wheat hybrids, but it would not explain the greater fertility found in pentaploid wheat hybrids. Possibly the greater number of bivalents in pentaploid hybrids would permit normal development of gametes with an excess or deficiency of several univalents necessary for a diploid or triploid chromosome combination. If only gametes with 3 or 4 univalents, i. e., gametes with 17 or 18 chromosomes, failed to function, then somewhat more than half of the gametes would be sterile, which in general would agree with the degree of sterility in the F_1. Gametes with larger chromosome numbers might be expected to develop with a greater deviation from the normal gametic number than gametes with a small number of bivalents. In the F_2 individuals the number of univalents would never exceed the ratio found in the F_1 if homologous chromosomes always pair. If then sterility is due to the ratio of univalents to bivalents, the F_2 individuals would never be more sterile than the F_1.

On the other hand, it is probable that more than the mere numerical relations of the chromosomes is involved in the sterility of wheat hybrids. The great differences in morphological and physiological characters indicate that the chromosomes of the various species are unlike. The

different wheat groups have existed for long periods of time, apparently without the formation of intermediate types, so that the chromosome constitutions may differ greatly even though the polyploid species have originated by reduplication of the diploid set of a primary species. In the pentaploid F_1 hybrid the 14 chromosomes of the Emmer group presumably pair with the allelomorphs of the Vulgare group which they most nearly resemble. The 7 univalents would then perhaps contain factors primarily characteristic of the Vulgare species. If we assume that the members of the bivalent chromosomes can be interchanged in most cases without causing non-functional chromosome combinations, most of the sterility will be caused by the abnormal behavior of the univalent chromosomes. Gametes with 14 chromosomes, and with perhaps 1 or 2 additional univalents, would be fertile and would carry an excess of Emmer factors, while gametes with 21, 20 or 19 chromosomes would carry largely Vulgare factors. The assumption that gametes with 3 or 4 univalents do not develop is in accord with the cytological finding of KIHARA in F_3 segregates. The fertility increases as the chromosome number progresses from 38 to 42. Some 28-chromosome segregates were highly sterile. This latter case may be due to incompatible relations of the members of the 14 bivalent chromosomes. If therefore chromosome mixtures in the bivalents sometimes disturb gametic development,—although in most cases normal development is correlated with an increase or decrease in number of univalent chromosomes, with greatest fertility in 28- and 42-chromosome individuals,—then most of the data both on character transmission and on sterility can be explained. The union of similar gametes would produce segregates with a predominance of either Emmer or Vulgare characters. Intermediates would be formed by a union of the more extreme types. As a result there would be partial linkage of Emmer characters and of Vulgare characters, although pure parental types would rarely be recovered. A preliminary examination of the genetic data indicates that in the F_2 segregates of an Emmer-Vulgare cross many characters are partially linked. It would be possible only in rare cases therefore to combine the Emmer and Vulgare characters in a fertile homozygous individual. In order to explain why varieties or species with intermediate chromosome numbers such as 34 or 36 are not found, it is necessary to assume further that even the bivalent chromosomes cause sterility unless a complete set is present.

If a complete set of chromosomes is essential not only for gametic but also for somatic development, the greater sterility in F_2 could be explained on the ground that plants without a complete set of diploid

or triploid chromosomes vary directly in vegetative development with the completeness of chromosome constitution. In the F_1 two complete sets of chromosomes are present, so that somatic development is normal or is even increased through heterosis. In the F_2 the absence of certain chromosomes may result in various degrees of vegetative development, from plants that do not pass the rosette stage to plants which head out but are poorly developed. *In F_1 sterility is apparently due only to gametic chromosome combinations but in F_2 individuals a weak somatic development would prevent gamete formation although such formation might be possible on a normal plant. Thus the greater sterility in F_2 can be attributed, not to greater gametic sterility, but to a combination of somatic and gametic functions.* The fact that there is a rather high degree of negative correlation between sterility and size of plant indicates that much of the F_2 sterility is due to unfavorable vegetative development of the F_2 individuals.

The assumption that gametes are formed with a predominance of Emmer or of Vulgare factors in the F_1, would explain the absence of homozygous segregates combining the desirable characters of the two different groups. Many hybrids between members of the Vulgare and Emmer group have been made, but few if any of the segregates have contained the desired combinations of parental characters in a homozygous condition.

The above explanation would also agree with the hereditary behavior in F_2.[1] We would expect segregates to form in 3 classes, those with predominance of Emmer characters, those with predominance of Vulgare characters, and those with union of the two types. The latter class of segregates might be considerably reduced by sterility. In the F_2 we actually find considerable linkage of characters. In the F_2 of Amby $\times$ Kubanka the type of culm, whether solid or hollow, is partially correlated with length of glume, compactness of spikelet, carination of glume, glume color, pubescence, compactness of head, color of grain and texture of grain. It appears that the 17 characters described can be classed in 3 or 4 partially linked groups. Similar relations are found in other crosses. For instance in a cross of Marquis $\times$ Alaska with hollow and pithy

[1] The genetic results here summarized were obtained from an investigation in progress by Dr. GAINES and the writer. Five partially sterile hybrids were grown in the F_2 with a total of 714 individuals. The characters of the F_2 individuals were described and the data were punched on cards and analyzed with the aid of a sorting machine. In two crosses, involving descriptions of 17 characters, each character was correlated with every other character to determine the correlation between the various characters and the correlation of characters with sterility.

straw and hard and soft grain, respectively, there is a high degree of correlation between type of culm and hardness of grain ($r = .48 \pm .04$). It is possible, of course, that the high degree of association of parental characters found in these species crosses is due to chromosome linkage or in some cases to multiple effects of a single factor, but crosses within the Vulgare group have shown only a few linked characters. In either case the association of parental characters indicates the difficulty in combining the desirable characters of the Emmer and Vulgare groups.

The correlation between sterility, as indicated by grains per spikelet, and the number of heterozygous factors in F_2 individuals, should be relatively high if the F_1 gametes are predominantly Emmer or Vulgare in functional composition. Two classes of gametes, consisting largely of factors from either parent, would also be found if EAST's (1915) hypothesis (B) is used to interpret the results. In either case the general method of gamete function is essentially the same, and in the F_2 the segregates resembling the parents should be relatively fertile while those intermediate like the F_1 should be relatively sterile. The correlation between sterility and number of heterozygous factors in an F_2 of *T. vulgare* × *T. turgidum* was found to be practically zero ($r = .03 \pm .06$). Similar results were obtained in other partially sterile wheat hybrids. If most of the 17 characters analyzed are dependent on factors in 2 or 3 chromosomes, little or no correlation would be expected between sterility and number of heterozygous factors.

Although many of the cytological and genetic facts are in accord with the sterility hypothesis presented, more work is necessary to put the chromosome and sterility relationships on a sound basis. Especially is more cytological work necessary in analyzing F_2 individuals. KIHARA (1921) has obtained chromosome counts of 8 F_2 plants in a partially sterile wheat cross and finds the chromosome number ranges from 31 to 42, but not in the frequency that would be expected. KIHARA believes that in the formation of an F_2 plant at least one gamete must have a complete set of either 14 or 21 chromosomes, but if all combinations of univalents and bivalents in the gametes are viable, as KIHARA apparently assumes, and if there is no selective fertilization, then only about 3 percent of the zygotes would develop. Moreover, if the sterility relationships depend on more than mere numerical ratios, and certain specific chromosome combinations cannot function, the degree of fertility will be greatly decreased. If, for instance, all 14 chromosomes of a 14-chromosome gamete must be from the Emmer parent, as KIHARA apparently assumes, then only one gamete in 16,384 would be functional in the F_1

plant. In any case, KIHARA's hypothesis is not in accord with either the cytological facts or with genetic results.

It appears that sterility in wheat hybrids is caused by other factors than those involved in partially sterile Nicotiana hybrids (EAST 1915). In wheat hybrids the abnormal behavior of chromosomes is associated with sterility, although incompatible chromosome combinations probably are factors as in the case of Nicotiana hybrids.

The origin of tetraploidy and hexaploidy in wheat species

The fact that the gametic chromosome number in the species of wheat are in multiples of 7 suggests that the tetraploid and hexaploid species are derived from a primary diploid species by chromosome reduplication. This view is also supported by the fact that several characters are dependent on 2 or 3 independent factors resulting in F_2 ratios of 15 : 1 and 63 : 1. It is also significant that the nearly related cereals have similar chromosome numbers. Rye has 7 haploid chromosomes and in the genus Avena, species are found with 7, 14 and 21 gametic chromosomes (KIHARA 1919). In other genera with polyploid species the tetraploid forms are in most cases known to have originated by chromosome duplication. In the wheat species and in certain other cases there is a striking correlation between chromosome number and cell size, which would indicate that the higher chromosome numbers are the result of duplication and not transverse fragmentation.

On the other hand there is evidence that does not support the view that tetraploidy and hexaploidy in wheat is actually due to chromosomal duplication. In cases where tetraploidy has occurred under experimental conditions the reduplicated sets of chromosomes assort at random in reduction which is not the case in tetraploid wheat species.

If the Emmer and Vulgare groups are the result of polyploidy, then, most if not all characters should be dependent on multiple factors. Of the characters which have been genetically investigated in wheat, 14 are apparently dependent on 1 factor, 4 characters behave as dihybrids, and only 1 character, red grain color, is clearly due to 3 independent factors in some cases. The latter character may also depend on only 1 or 2 factors in certain varieties. In wheat species, where the chromosomes of the polysomic sets assort in pairs, mutations could result in characters dependent on 1 or 2 factors; but in tetraploid species, where the chromosomes of a tetrasomic set assort at random, a single factor could not exist in the homozygous condition. It is possible that chromosomal duplication

occurred very early in the history of cultivated wheat and that in the course of time the individual chromosomes came to differ so that they no longer assorted at random within a reduplicated set.

Representations of all of the three groups of wheat can be traced back to prehistoric times (PERCIVAL 1921). Einkorn was probably one of the chief wheats grown in central Europe in the Neolithic period. Emmer was grown in Europe in prehistoric times and was grown in Egypt as early as 5400 B. C. It was the most important cereal in Egypt from the early ages until supplanted by Durum and Vulgare varieties in the Graeco-Roman period. Although representatives of the Vulgare wheat group were known to exist in Europe in prehistoric ages they were not the chief varieties grown until comparatively recent times. The great age of the three wheat groups may also explain why the groups differ so markedly in morphological characters even if they were originally derived from a single primary species by chromosome duplication. Although the species within each group overlap considerably, the differences between the three sterility groups are rather distinct. PERCIVAL has summarized the important characters which differentiate the Vulgare group from the Emmer group as follows: (1) Differences in arrangement of hairs on the leaf; (2) thin-walled, hollow culms; (3) a tough, non-disarticulating rachis; (4) absence of keel on the lower part of the glume in most cases; and (5) the comparatively short awns of the fully bearded varieties and the occurrence of beardless and semi-bearded varieties. The greatest difference is, of course, the high quality of the gluten in most of the Vulgare varieties. No variety of the Emmer group contains gluten of the quality necessary for the production of light spongy bread. The species of the Emmer group are, in general, best adapted to a hot dry climate, and because of susceptibility to cold weather, they are in few cases sown in the fall in the temperate zone.

Many of the characters which distinguish the Vulgare from the Emmer group are found in *T. aegilops ovata* or *T. aegilops cylindrica* and accordingly PERCIVAL has concluded that the Vulgare group is a hybrid race resulting from an early cross or crosses of members of the Emmer group and *T. aegilops*. The hybrids of the present species of the Emmer group or even *T. dicoccoides* with *T. aegilops* are, however, nearly or quite sterile in the F_1.

Chromosome number and adaptability in wheat species

The characters of the Vulgare group are subject to very wide variation and the great number of varieties and intermediate forms are believed by

PERCIVAL to be due to their hybrid origin. The great variability and adaptability of the Vulgare wheats may, however, be due to other causes. EAST (1915) suggested that variability of a species would be correlated with the chromosome number and DORSEY in 1916 suggested that the adaptability of a species might be correlated with chromosome number. With an increase of chromosome number the number of factorial combinations would increase, thus resulting in a greater range of adaptation. There is certainly a high degree of correlation between chromosome number and adaptability in the species of wheat. The number and distribution of the varieties of the cultivated species of wheat are shown in table 7.

TABLE 7

Number and distribution of varieties of the Einkorn, Emmer and Vulgare groups. (*Data from* PERCIVAL 1921.)

	T. monococcum	*T. dicoccum*	*T. durum*	*T. polonicum*	*T. turgidum*	*T. pyramidale*	*T. vulgare*	*T. compactum*	*T. sphaerococcum*	*T. Spelta*
Number of "varieties"	3	40	22	23	27	5	26	20	6	12
Groups		Emmer					Vulgare			
Haploid chromosome number	7	14					21			
Distribution of "forms"										
S. E. Europe, S. W. Asia	*	10					9			
Southern Europe	*	77					42			
Russia		7					12			
Central and N. Europe		27					102			
England		13					91			
India		2					4			
Australia and New Zealand		3					63			
South Africa		4					23			
Japan and China							11			
North America		7					109			
South America		1					7			
Total		151					536			

*Species of Einkorn grown but no cultivated "forms" described.

PERCIVAL (1921) recognizes only two wheat species, *T. aegilopoides* and *T. dicoccoides*, and suggests that the other types might be classed as

"cultivated species." Under the term "forms" PERCIVAL classes what are commonly known as varieties, such as Marquis, Bluestem, Kubanka, etc. It will be seen in table 7 that the number of the varieties is greatest in the Emmer group, but that the Vulgare group contains almost four times as many "forms." The distribution of the different groups is also significant. The members of the Einkorn and Emmer groups are found in greatest numbers in the regions where wheat originated. In general the region has a warm dry climate. The members of the Emmer group are comparatively rare in Australia, England, South Africa, Japan and North America. Members of the Vulgare group are found all over the world wherever wheat is grown and under diverse climatic conditions. Although the Vulgare group is more variable and adapted to a greater range of conditions they are not always the highest yielders. Certain varieties of *T. turgidum* are the most productive of all wheats, and under certain conditions varieties of *T. durum* will outyield the Vulgare varieties. The correlation between chromosome number and adaptability in wheat species may not depend on a causal relationship. The Vulgare group may be more highly selected and more widely distributed because it is the only wheat suitable for making light bread. The greater variation and adaptability would also be expected if the Vulgare group is a vast hybrid race as PERCIVAL has suggested. A study of chromosome number in relation to variations and adaptability in polyploid species under natural conditions would be of interest.

The value of tetraploidy

Since tetraploidy usually results in increased size of plant tissues and possibly permits greater adaptability, the development of tetraploid species may be of value. WINKLER (1916) has obtained tetraploid forms of tomatoes and nightshade in connection with his work on graft hybrids. The tetraploid forms were larger than diploid forms but unfortunately they were sterile. A number of investigators have been able to induce changes in the chromosome number of somatic cells by treatment with various reagents (SAKAMURA 1920) but it appears to be questionable if such changes can be maintained and established in later generations. CASTLE (1921) has suggested that the French prune mutation described by SHAMEL (1919) is the result of tetraploidy. It is not improbable that the best cases of bud mutations involving increased productivity (if such mutations actually occur) will be found to be associated with tetraploidy or chromosome duplication.

DESCRIPTION OF PLATES

Preparations from pollen mother cells at the time of the reduction divisions. The drawings were made with the aid of a camera lucida. All figures were drawn from single sections. Magnification 750 diameters. No reduction. The reproduction of these drawings has been made possible by financial assistance from BUSSEY INSTITUTION.

PLATE 1

Triticum monococcum

FIGURE 1.—The 7 paired chromosomes at diakinesis.
FIGURE 2.—Metaphase, polar view. Heterotypic division.
FIGURE 3.—Metaphase, side view.
FIGURE 4.—Late anaphase, 7 chromosomes at each pole.
FIGURE 5.—Polar view of late anaphase showing the 7 chromosomes split for the homoeotypic division.
FIGURE 6.—Telophase of the homoeotypic division.

The Emmer group

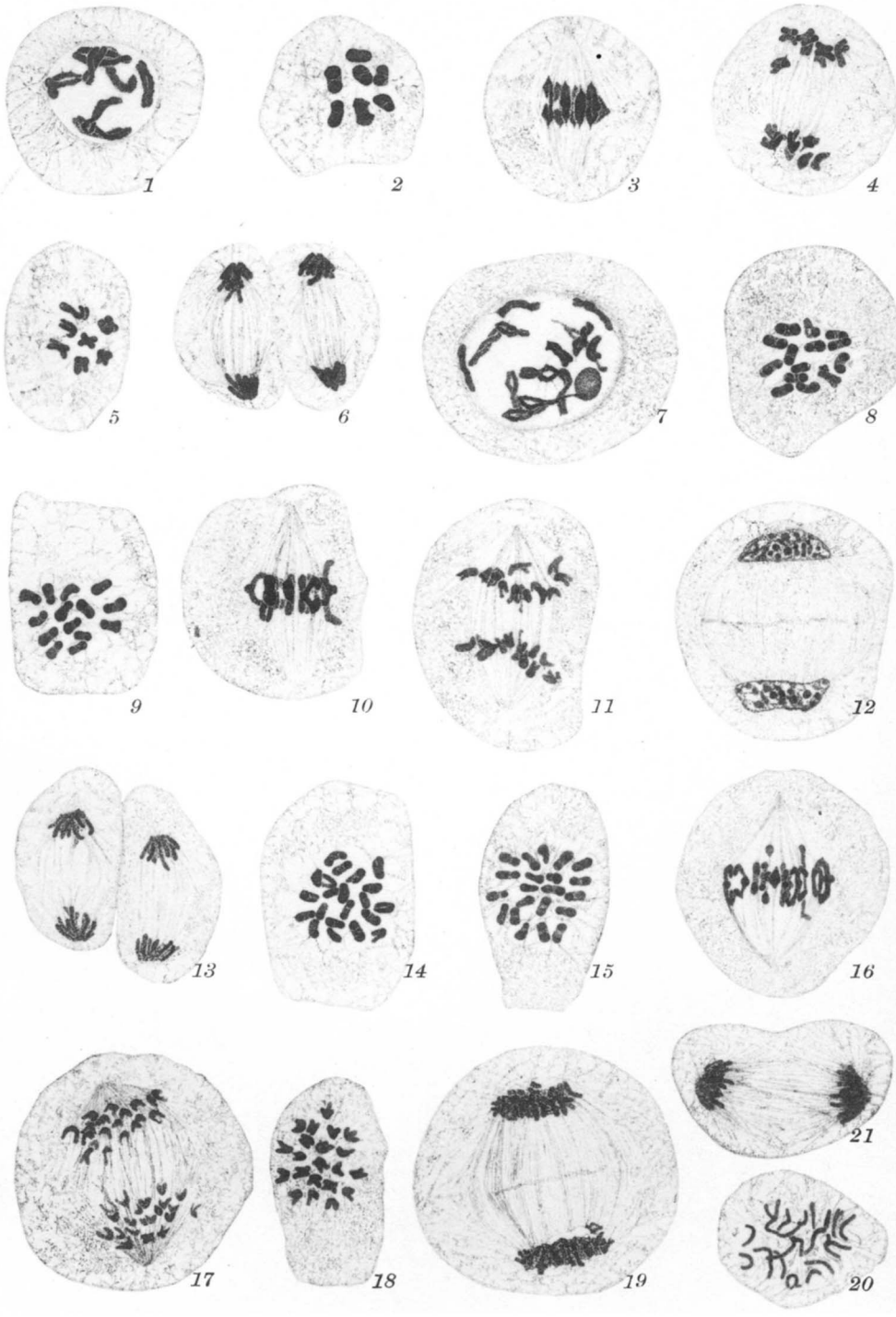
FIGURE 7.—Diakinesis. 14 pairs of chromosomes. *T. durum.*
FIGURE 8.—Metaphase, polar view. 14 chromosomes.

T. polonicum

FIGURE 9.—Metaphase, polar view. *T. durum.*
FIGURE 10.—Metaphase, side view. *T. polonicum.*
FIGURE 11.—Anaphase of heterotypic division. *T. polonicum.*
FIGURE 12.—Interkinesis. Resting nuclei. *T. polonicum.*
FIGURE 13.—Telophase of homoeotypic division. *T. durum.*

The Vulgare group

FIGURE 14.—Metaphase, polar view. 21 chromosomes. *T. Spelta.*
FIGURE 15.—Metaphase, polar view. 21 chromosomes. *T. vulgare.* (Preston)
FIGURE 16.—Metaphase, side view. *T. vulgare.* (Preston)
FIGURE 17.—Late anaphase of heterotypic division, side view. *T. vulgare.* (Preston)
FIGURE 18.—Late anaphase, polar view. *T. vulgare.* (Preston)
FIGURE 19.—Telophase. *T. vulgare.* (Marquis)
FIGURE 20.—Metaphase. Homoeotypic division, polar view. *T. vulgare.* (Amby)
FIGURE 21.—Telophase, homoeotypic division. *T. vulgare.* (Amby)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The value of polyploidy may have certain limitations. As TUPPER and BARTLETT (1918) have suggested, a few doublings in chromosome number would increase the size of the cell so that respiration and nutrition would be retarded. In Crepis and Chrysanthemum, however, the chromosome number has apparently been duplicated many times without disastrous results. MULLER (1918) believes that tetraploidy would hinder evolution because recessive mutants could rarely manifest themselves. If recessive factors have some effect in the presence of dominant factors, which is frequently or perhaps usually the case, then increased variability would result even if the pure recessive could rarely be isolated.

There has been considerable discussion as to the origin of tetraploid species especially in Oenothera. GATES (1915) argues that *Oe. gigas* must have originated by a doubling of chromosomes at an early stage in somatic development of a diploid species, because of the rare occurrence of diploid gametes. This interpretation is undoubtedly the most reasonable in cases where tetraploid individuals have suddenly originated from a diploid species. If a diploid gamete united with a normal haploid gamete and the chromosomes in the trisomic sets assorted at random 25 percent of the F_2 segregates would be tetraploid. The occasional occurrence of diploid gametes has been observed in several diploid species and would afford an opportunity for the formation of tetraploid species although the latter would originate from a triploid individual and not directly from the original diploid species.

Pollen-grain variability

The pollen of F_1 plants of species hybrids is much more variable than the pollen of pure species.

The remarkable relation between heterosis or degree of germinal mixture and variability of pollen grains is especially interesting because the pollen grains belong to the gametophytic generation. In most cases recorded the characters of the pollen grain are determined by the mother plant. BATESON (1909) has found that the shape and color of pollen in the sweet pea behave as sporophytic characters. EAST (1916) has found a similar behavior of pollen in Nicotiana and also finds that self-sterility behaves as a sporophytic character (EAST 1919). On the other hand BELLING (1914) has found segregation of normal and aborted pollen grains in semi-sterile F_1 hybrids, and PARNELL (1921) finds segregation of equal numbers of starchy and glutinous pollen grains in an F_1 rice hybrid. The occurrence of the starchy and glutinous pollen grains

DESCRIPTION OF PLATE 2

T. monococcum (7-chromosome gametes) × *T. turgidum* (14-chromosome gametes)

FIGURE 22.—Metaphase of heterotypic division with 7 bivalents (1 divided) and 7 univalents at the poles.

FIGURE 23.—Late anaphase with approximately 10 chromosomes at either pole due to the division of the bivalents and the random assortment of the univalents without dividing.

FIGURE 24.—Early telophase. Split chromosomes, originally members of the bivalent chromosomes, just reaching the poles.

FIGURE 25.—Telophase. No lagging chromosomes.

FIGURE 26.—Anaphase of homoeotypic division. Vulgare group (21-chromosome gametes) × Emmer group (14-chromosome gametes), F_1 plants.

FIGURE 27.—Metaphase, polar view, of homoeotypic division with about 10 chromosomes in each figure.

FIGURE 28.—Metaphase of heterotypic division, polar view. Fourteen bivalents and 7 univalents. Amby × Kubanka.

FIGURE 29.—Metaphase showing bivalents and univalents. Bluestem × Alaska.

FIGURE 30.—Metaphase of heterotypic division showing irregularly distributed univalents. Note the attachment of the spindle fibers and apparent tension of the chromosomes. Amby × Kubanka.

FIGURE 31.—The bivalents have divided leaving the 7 univalents and apparently several additional unpaired chromosomes on the equatorial plate. Amby × Kubanka.

FIGURE 32.—The 14 bivalents have divided and reached the poles while the 7 univalents are dividing equationally. Amby × Kubanka.

FIGURE 33.—A similar stage in Bluestem × Kubanka.

FIGURE 34.—A similar stage in Bluestem × Kubanka.

FIGURE 35.—The 7 univalents have divided and have nearly reached the poles. Bluestem × Alaska.

FIGURE 36.—Homoeotypic division showing univalents which do not divide but pass at random to either pole and join the original 14 bivalents.

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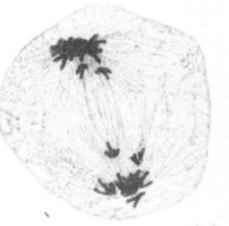

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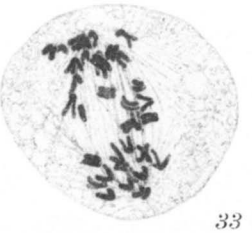

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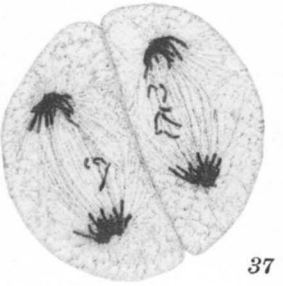

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is undoubtedly due to the effect of the segregated factors. In the wheat hybrids the factors for growth apparently segregate into various proportions of maternal and paternal factors in the F_1 and the various combinations of these factors may cause increasd variation in size of pollen grains, ranging from completely aborted grains to those much larger than normal. The increased variability is due here to combinations of non-homologous chromosomes acting in the gametophytic generation and to differences in chromosome number. In cases where the gametophytic characters are controlled by the sporophyte the characters may be those primarily caused by the sporophyte, such as pollen-grain shape and possibly color. In other cases certain characters, such as growth and starch-formation, may be controlled by the gametophytic chromosomes at an early stage in the development of the gametophyte, while perhaps other characters cannot be brought into expression until the necessary development of the organism has been attained.

SUMMARY

The chromosome number and behavior has been determined for the cultural species of Triticum and for certain partially sterile hybrids.

The gametic chromosome number is 7 for *T. monococcum*; 14 for the Emmer group, consisting of *T. dicoccum*, *T. durum*, *T. polonicum*, and *T. turgidum;* and 21 for the Vulgare group, consisting of *T. vulgare*, *T. compactum* and *T. Spelta*. Rye (*Secale cereale*) has 7 gametic chromosomes.

In the F_1 hybrid of *T. monococcum* × *T. turgidum* 7 chromosomes are contributed by one parent and 14 by the other parent. In the heterotypic division of the pollen mother cells there are 7 bivalents and 7 single chromosomes. The 7 bivalents divide normally, but the 7 univalents pass at random to either pole without dividing. In the homoeotypic division there are usually about 10 or 11 chromosomes which apparently divide normally in most cases. Tetrads and one-nucleate pollen grains appear to be normal, but very few normal mature pollen grains are formed.

In F_1 hybrids between members of the Emmer group and members of the Vulgare group, 14 chromosomes are contributed by one parent and 21 by the other parent. In the first meiotic division there are 14 bivalent and 7 univalent chromosomes. The bivalents divide normally, but the univalents do not become oriented on the equatorial plate until the bivalents have divided. The 7 lagging univalents divide equationally and 7 chromosomes pass to each pole. In the homoeotypic division the

DESCRIPTION OF PLATE 3

Micro-photographs of chromosomes in the reduction divisions of the pollen mother cells in wheat species, rye, and wheat hybrids. Photographs not retouched.

FIGURE 37.—Late anaphase showing the 7 chromosomes in Einkorn.

FIGURE 38.—Late anaphase, side view. Einkorn.

FIGURE 39.—Late anaphase with 14 chromosomes at one pole. Polish.

FIGURE 40.—Metaphase, polar view. 21 chromosomes. Preston.

FIGURE 41 A, B.—Diakinesis in rye, showing the 7 pairs of twisted chromosomes.

FIGURE 42.—Metaphase showing univalents and bivalents in (Amby × Kubanka) F_1.

FIGURE 43.—Bivalent chromosomes have divided and reached the poles while the split univalents are on the heterotypic plate. (Amby × Kubanka) F_1.

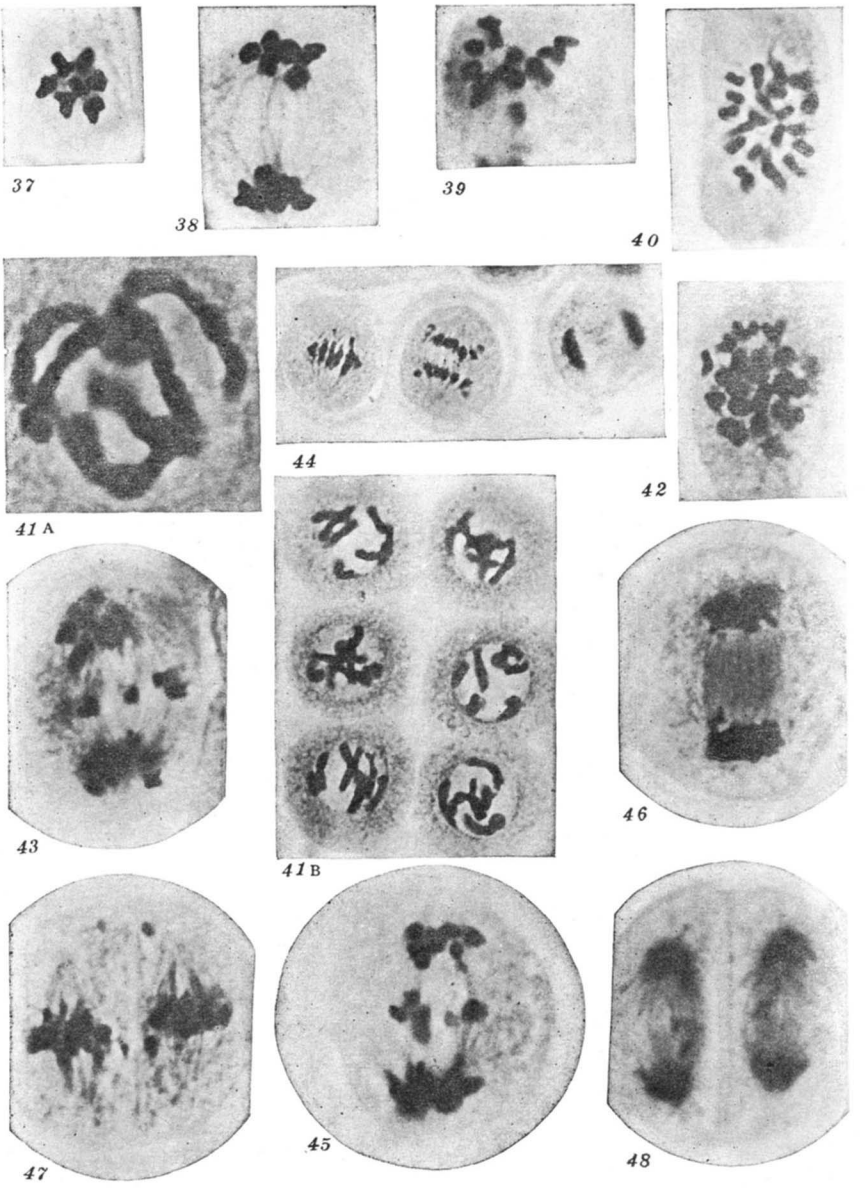
FIGURE 44.—Metaphase, anaphase, and telophase in 3 adjacent pollen mother cells in an anther of Preston.

FIGURE 45.—Same as figure 43.

FIGURE 46.—Telophase, no lagging chromosomes. (Amby × Kubanka) F_1.

FIGURE 47.—Metaphase, side view of the homoeotypic division showing several irregularly distributed chromosomes. (Amby × Kubanka) F_1.

FIGURE 48.—Homoeotypic division showing lagging chromosomes. Same as figure 36. Amby × Kubanka) F_1.



J. W. B. and K. S. photo.

original members of the bivalents divide normally, but the remaining 7 chromosomes pass at random to either pole without dividing. As a result the chromosome number of the microspores varies from 14 to 21. The tetrads and one-nucleate pollen grains appear to be normal, but in later stages about 20 percent of the pollen grains are obviously imperfect and undoubtedly a larger percentage is non-functional.

The size of the pollen grains is closely correlated with the chromosome number in the various species of wheat.

The pollen grains of fertile species hybrids are more variable than the pollen grains of the parental species due to various degrees of compatibility of the combinations of non-homologous chromosomes in the gametophytic generation. In partially sterile hybrids where the parental species differ in chromosome number, the pollen grains are extremely variable, due to difference in chromosome number and to more or less compatible chromosome combinations.

The sterility in the hybrids described can be accounted for on a hypothesis involving, (1) the numerical or unbalanced relations of the chromosomes resulting from the irregular meiotic divisions, and (2) the specific interrelations of the parental chromosomes. In the numerical relations the development of gametes varies as the chromosome number approaches the normal gametic number (7, 14 or 21). It is assumed that the greater the gametic chromosome number the greater can be the deviation from the normal number. The specific relations of the gametic chromosomes will depend on the extent that chromosomes from one parent can be substituted for those of the other parent. Gametic perfection will vary as the chromosome constitution approaches that of the parental forms. The 7 univalents in the Emmer-Vulgare F_1 hybrids presumably carry most of the factors which differentiate the Vulgare characters from the Emmer characters.

This hypothesis will explain (1) the differences in sterility of the various species hybrids, (2) the partial association of the original parental characters in the F_2 segregates, (3) the absence of varieties or species with intermediate chromosome numbers, and (4) the difficulty in obtaining homozygous segregates combining the desirable characters of the parental species in partially sterile wheat hybrids.

In all cases the F_1 plants are unusually vigorous and sterility is not due to poor vegetative development, but is caused by the formation of non-functional gametes. Sterility in F_2 segregates may be greater than in F_1 individuals due, not to greater gametic sterility *per se*, but to a combination of weak somatic development and gametic sterility.

The evidence for and against the occurrence of chromosome duplication in wheat species is presented and discussed.

There is a high degree of correlation between chromosome number and adaptability in the wheat species, but the relation may not be a causal one.

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