CYTOLOGY AND GENETICS OF CROSSES BETWEEN FOURTEEN- AND SEVEN-CHROMOSOME SPECIES OF WHEAT

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Crosses between species of Triticum belonging to the emmer group ($n=14$) and ones belonging to the *vulgare* group ($n=21$) have been investigated extensively and profitably from the cytological standpoint, but those between emmers and einkorns ($n=7$) have hitherto been studied only in the first generation. The very high degree of sterility of F_1 of the latter type has presumably made it difficult to secure a sufficient number of plants of later generations. Recently, however, a considerable amount of material has become available and is the subject of the present report.

REVIEW OF BEHAVIOR IN F_1

In order to interpret the results obtained with plants of later generations it will be necessary to refer to the cytology of F_1. In the hybrid between *T. turgidum* ($n=14$) and *T. monococcum* ($n=7$) SAX (1922) found that 7 chromosomes from *turgidum* paired with those of *monococcum* and that the other 7 were left unpaired. The latter failed to move into the central position and remained intact at the heterotypic division, but divided at the homotypic. In a cross between other varieties of the same two species THOMPSON (1926) found the behavior to be quite different. The number of conjugated pairs varied from 3 to 7, the commonest being 5. Consequently the univalents varied from 7 to 15. Usually all of the latter and always the majority of them moved to the equator after the bivalents and divided at the first division, as do those of other wheat hybrids. At the homotypic division the number of lagging univalents was quite variable, depending on the amount of non-conjunction at the previous division and on the number of univalents which had failed to move into the plate. Consequently the number of chromosomes in individual pollen grains must have varied widely. Usually it would be 10 or 11. But if only 3 pairs had mated at the first division and if all univalents had reached the same pole at the second, it would be as low as 3 or as high as 18.

Since that account was published hybrids between *monococcum* and *dicoccum*, *durum* and *polonicum* have been examined and in all of them the behavior was found to be the same as in *turgidum*×*monococcum*. Similar behavior was observed also by KIHARA and NISHIYAMA (1928) in *dicoccum* ×*monococcum* and by AASE (1930) in *durum*×*monococcum* and *dicoccoides* ×*monococcum*. It must therefore be regarded as the usual type in F_1 hybrids between 14- and 7-chromosome wheats.

METHODS

Owing to a large and variable amount of non-conjunction in plants of later generations and difficulty in distinguishing all univalents from bivalents at the heterotypic metaphase, it was very desirable to have polar views of the heterotypic anaphase for determining the total (somatic) number as well as the amount of pairing. In smear preparations only a small fraction of the cells presented polar views, because the axis of division was the long axis of the cells, which naturally tended to lie on their sides. Consequently in many cases paraffin sections had to be used. When these were cut transversely to the long axis of the stamen most of the mother cells presented polar views, and when they were at anaphase counting of both groups of bivalents and the intervening univalents presented little difficulty. In all cases, however, smears were first made because they were excellent for determining the frequency of the different numbers of univalents, and if the amount of pairing was fairly constant and the total number not too large, complete determinations could usually be made from them alone. Part of the fixed material of each plant, preserved in 70 percent alcohol, was therefore first examined in smears, and in case the results were doubtful the rest was imbedded and sectioned.

The 7-chromosome species used was *T. monococcum* and the 14-chromosome species *T. durum* and *T. turgidum*.

FERTILITY

Using the average number of spikes per plant and of flowers per spike, and the total number of grains obtained, it is estimated roughly that about 1 F_1 flower in 800 or 900 formed a grain when the plants were grown unprotected in an ordinary plot near other wheat plants. Most of the grains were the product of self-pollination which is the rule in wheat, but some resulted from natural cross-pollination which was favored by the high degree of sterility. When the first lot of F_1 were grown, protection was neglected because of the habitual self-pollination of the parents. When the spikes were bagged the number of grains was somewhat reduced, but evidently gametes of both sexes were capable of functioning.

More than 98 percent of the F_1 pollen grains were shrunken and without contents.

Some results of artificial backcrossing are given in table 1. It appears that the F_1 cannot be backcrossed either as male or female with the 7-chromosome parent. With the 14-chromosome parent the female gametes were more fertile than the male, but in both the fertility was very low. Consequently the labor involved was too great to secure, by artificial back-pollination, a sufficient number of offspring for a comprehensive study. The F_1 themselves, however, can be produced in large numbers, and when grown well spaced in favorable conditions bear an immense number of flowers from which a reasonable number of grains may be secured.

TABLE 1

Results of backcrossing.

BACKCROSS	FLOWERS POLLINATED	GRAINS FORMED
F_1 ♀ × *monococcum* ♂	390	0
monococcum ♀ × F_1 ♂	440	0
F_1 ♀ × *durum* ♂	365	3
durum ♀ × F_1 ♂	258	1

CHROMOSOMES IN F_2

The somatic chromosome numbers of 41 F_2 plants are given in table 2. It may be observed that nearly all had 28 or more chromosomes, that is, as many as or more than the parental species with the larger number, and that the remainder had only 1 or 2 fewer. No plant with a number approaching that of *monococcum* ($2n = 14$) was found.

This result is quite different from that obtained by several investigators

TABLE 2

Somatic chromosome numbers in F_2.

CROSS	CHROMOSOME NUMBERS							
	26	27	28	29	30	35	36	42
durum (28)×*monococcum* (14)	1	2	11	6	2	2	..	2
turgidum (28)×*monococcum* (14)	..	1	6	2	1	3	2	..
Total	1	3	17	8	3	5	2	2

in crosses between 28- and 42-chromosome (2n) species. In those, segregates with various numbers between 28 and 42 were found. In some crosses of that kind, and perhaps in all, there were far more segregates with the lower number of the emmer parent than with the higher number of the *vulgare* parent (THOMPSON and HOLLINGSHEAD 1927).

In the pollen mother cells of the majority of F_2 of the present crosses

TABLE 3

Number of univalent chromosomes observed in pollen mother cells of some individual F_2 plants.

SOMATIC NUMBER	UNIVALENTS OBSERVED IN POLLEN MOTHER CELLS	
	COMMONEST NUMBER	LARGEST NUMBER
26	2	4
27	1	3
	3	5
28	0	1
	0	2
	0	4
	0	5
	2	2
	2	4
	2	8
29	1	1
	1	2
	1	3
	1	5
	3	3
	3	7
30	2	4
	2	10

there was considerable variation in the number of chromosomes which paired, and consequently in the number of lagging univalents. Table 3 shows the commonest number of univalents observed and also the largest number in some individual F_2, the somatic numbers of which are shown in the column at the left. Table 4 shows the frequency distribution of the numbers of univalents seen in several plants. The number of univalents seen in any particular cell may not have been all there were in that cell, owing to their being obscured by bivalents at metaphase, or to their failure to move into the central region after the bivalents had divided. The only chromosomes recorded as univalents were those concerning which there could be no doubt.

TABLE 4

Frequencies of different numbers of univalents in certain F_2.

SOMATIC NUMBER	UNIVALENTS													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
26	5	3	38	..	4	..	..	..	..	..	..	..	..	..
27	..	1	4	19	2	7	..	..	..	..	..	..	..	..
28	25	1	2	..	..	..	..	..	..	..	..	..	..	..
	18	5	15	..	..	..	..	..	..	..	..	..	..	..
	3	..	17	4	10	3	8	1	2	..	..	..	..	..
29	2	20	2	2	..	..	..	..	..	..	..	..	..	..
	12	25	6	16	3	4	..	..	..	..	..	..	..	..
	..	6	2	7	3	10	2	5	..	..	..	..	..	..
35	..	..	..	3	7	11	15	14	..	..	..	..	..	..
	..	..	..	..	1	2	6	13	1	4	..	2	..	..
36	..	..	..	..	..	..	2	11	16	8	1	2	1	1
42	21	11	10	5	8	1	3	1	..	..	..	..	..	..
	..	..	..	..	2	1	7	13	5	4	5	1	..	..

The tables show that different plants with the same somatic number exhibited quite different amounts of non-conjunction and different degrees of variability in the amount of non-conjunction. Thus in some 28-chromosome plants 14 bivalents and no univalents were usually seen, as was to be expected, although individual mother cells sometimes showed 1 or a few univalents. In other plants with 28 somatic chromosomes there were usually 2 univalents but frequently more than 2, and in one case as many as 8 were seen. Similar conditions prevailed in plants with other somatic numbers, but in general these were still more irregular. In many cases the number of univalents in a single stamen was so variable that it was difficult or impossible to decide what the normal number of pairs should be.

This variability is evidently related to the similar phenomenon in F_1 where 2 pairs often failed to conjoin and 3 or 4 pairs sometimes failed. It is conceivable that non-conjunction occurred about equally in the different pairs, now involving one pair and now another. But the F_2 results indicate rather that it occurred in certain pairs much more frequently than in others. If an F_2 plant received an emmer and a *monococcum* chromosome from such a pair it would presumably show much non-conjunction in this pair; if it received both members of the pair from emmer or from *monococcum*, it would show little. There are probably other factors also, because in some cases where there were usually no univalents or only one, sometimes a large number were seen.

In some plants trivalent chromosomes appeared to be frequent, but as it is often difficult to distinguish them from bivalents in this material with the methods used, no attempt was made to estimate their frequency. Their occurrence accounts for such observations as pollen mother cells without univalents in a 29-chromosome plant, the extra chromosome presumably having become attached to one of the bivalents.

Of the 41 plants, 5 had 35 chromosomes, 2 had 36, and 2 had 42. These plants may have been produced in 2 ways: (1) F_1 gametes with 21 chromosomes, the sum of the numbers in the parents, may have been formed and joined with similar gametes to produce 42-chromosome plants, or with 14- and 15-chromosome gametes to produce 35- and 36-chromosome zygotes respectively. (2) Pure *vulgare* male gametes, as a result of natural cross-pollination, may have fertilized 14-, 15-, or 21-chromosome F_1 eggs to produce 35-, 36-, or 42-chromosome plants respectively.

Some of the plants with 35-chromosomes and one of those with 42 had some *vulgare*-like characters and must have arisen as a result of out-crossing with some *vulgare* type, unless the combination of emmer and *monococcum* genes could produce *vulgare* characters. But the characters of the remainder including one 42-chromosome plant were such that they could not have had a *vulgare* parent. Consequently a considerable number of 21-chromosome F_1 gametes must have functioned. On any interpretation 2 F_1 eggs with 21 chromosomes must have functioned in order to produce 42-chromosome plants. In this connection attention may also be called to the facts that nearly half the mother cells of one 42-chromosome plant showed no unmated univalents and that the great majority had less than 3. If it had resulted from the fertilization of a 21-chromosome F_1 egg by *vulgare* pollen most of the mother cells would have shown at least 7 univalents, as is the case in the other 42-chromosome plant.

A hexaploid wheat plant and several pentaploids have therefore been produced by crossing a tetraploid with a diploid.

F_1 GAMETES WHICH FUNCTIONED

Ordinary gametes

The chromosome numbers of F_2 plants show that the great majority of F_1 gametes which functioned successfully must have had 14 chromosomes, the number in the gametes of the emmer parent, or more than 14. Those with 13 functioned rarely, those with 12 probably and with less than 12 certainly not at all in the material studied. In addition there were a few unexpected gametes with 21.

The theoretical frequencies of the F_1 gametes with the different chromosome numbers which are to be expected on the basis of the behavior at the meiotic divisions, are shown in table 5 for cases in which 7, 6, or 5 pairs conjugate. Mother cells with 5 bivalents are commonest; ones with 4 or 3 occur. In the commonest type (5II+11I) only 55 gametes among 2048 would have 14, 11 would have 15, and 1 would have 16. Obviously the great majority of the gametes—those with numbers from 5 to 12—were unable to function successfully.

TABLE 5

Chromosome numbers in F_1 gametes.

PAIRING IN MOTHERCELLS	5	6	7	8	9	10	11	12	13	14	15	16
7II+ 7I	..	..	1	7	21	35	35	21	7	1	..	..
6II+ 9I	..	1	9	36	84	126	126	84	36	9	1	..
5II+11I	1	11	55	165	330	462	462	330	165	55	11	1

This result is quite different from that obtained in hybrids between 14(n) and 21-chromosome wheats (THOMPSON and CAMERON 1928, SAX 1928). In those, some gametes with each number between 14 and 21 did function successfully, although most of the male ones and some of the female with intermediate numbers were inviable or unsuccessful. Moreover, those which had only 14 and therefore entirely lacked the differential set of 7 were quite viable; in fact they were more successful than those with 21. In the emmer-*monococcum* hybrids, on the other hand, those which lacked the differential set and consequently had only 7, were quite unsuccessful as shown by the fact that no F_2 with 14 somatic chromosomes or any number approaching 14 were found. Apparently combinations of emmer and *monococcum* chromosomes making up a set of 7 from those kinds which paired in F_1 were inviable unless an additional set of 7 was present. The failure of backcrossing with *monococcum* shows that F_1 gametes with 7 could not function even in association with healthy vigorous gametes which had the same number.

It is of course possible that gametes with fewer than 14 were actually capable of carrying on their function, but that the resulting zygotes perished. However the fact that more than 98 percent of the pollen was visibly abortive indicates that the sterility was gametic. Even many of those grains which appeared normal might be unable to function, particularly in view of the highly abnormal conditions in a stamen with so much bad pollen.

From the commonest type of mother cells (those with 5 bivalents and 11 univalents) only 55 gametes among 2048 would have 14 chromosomes. And it seems probable that most of these 55 would be unable to function. If we designate as AA′ and BB′ the 2 pairs which failed to conjoin, thereby giving 5II and 11I instead of 7II and 7I, it is probable that only those with 1A and 1B would be capable of functioning. If they had 2A's they must have lacked B's or 1 of the differential set of 7. At any rate, they would be more likely to function successfully than the others. There were only 4 such gametes among the 55 with 14 chromosomes. On the other hand, the occurrence of 28-chromosome F_2 in which 2 or more univalents were usually to be seen in the meiotic divisions may indicate that some other combinations could function.

If the mother cells had 6II and 9I, 9 of 512 gametes would have 14 and 1 would have 15 chromosomes. Only 2 of the 9 may be expected to have viable combinations. If the mother cells had 7II and 7I, 1 of 128 gametes would have 14 and none 15. The proportion of 14-chromosome gametes with each kind of chromosome represented once, which would be produced from the different kinds of mother cells, is as follows:

7II+ 7I	1 in 128
6II+ 9I	1 in 256
5II+11I	1 in 512
4II+13I	1 in 1024

If the theoretical fertility of F_1 be calculated by multiplying the proportion of 14-chromosome eggs by that of 14-chromosome pollen, a figure is obtained much lower than that actually found. But this method would be unwarranted because, owing to abortion of the pollen, the 14-chromosome grains have little competition. Each flower contains only 1 egg and each stigma receives many grains, some of which may have 14.

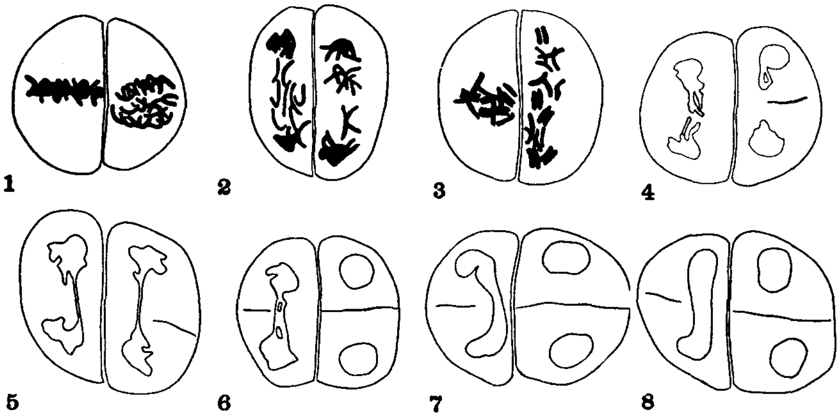
Gametes with restituted nuclei

In order to determine whether some special or abnormal process in the behavior of F_1 chromosomes might be increasing the proportion of 14-chromosome gametes, the meiotic division of F_1 were carefully reexamined in material from many stamens. A second reason for this reëxamination was the desirability of explaining the occurrence of 21-chromosome gametes. That the latter were not due to doubling of chromosomes in early somatic tissues was evident from the fact that the grains occurred singly in ears which were otherwise sterile.

The heterotypic division showed nothing of significance in this connection. The lagging univalents, numbering from 7 to 15, divided in regular fashion; the halves separated cleanly and followed the bivalents to the poles in an orderly row. In almost every case all the chromosomes became incorporated in the daughter nuclei; very rarely were any lost or were micronuclei formed. No indication of a restitution of the somatic number was observed in many hundreds of cells at this division. Owing to the regularity of the division in spite of the large number of univalents, restitution would be very unlikely to occur. Therefore the interphase nuclei, which were always separated by a wall, would have about 14 chromosomes (7 halves of bivalents $+$ 7 halves of univalents or $6+9$, or $5+11$). Occasionally the number would be somewhat smaller owing to 1 or a few univalents remaining undivided at one pole instead of moving into the plate.

The homotypic division, on the other hand, frequently presented significant appearances. It was usually very irregular. The halves of univalents remained for a long time in the central region, becoming much elongated, and moved very slowly and irregularly to the poles without dividing (figures 1 and 2). Usually the bivalents and the first univalents to arrive at the pole had formed the daughter nucleus while several univalents still remained outside; the latter then formed micronuclei. Partially incorporated univalents often connected the polar mass with one or more micronuclei. In many cases a series of univalents extended between the two daughter nuclei (figures 2, 4). Not uncommonly these formed a connecting bridge between the two nuclei at telophase and later. The bridge was usually slender (figure 5) but often nearly or quite as wide as the masses of chromatin at the ends (figures 6, 7). The chromosomes constituting the bridge passed into the resting stage in the same way as those at the poles. In this manner a single nucleus, at first usually dumb-bell shaped, was sometimes reconstituted following the homotypic division (figures 7, 8).

The bridge varied in width from that of a single chromosome to a wide band composed of a considerable number. It is to be remembered that the number of univalents might be as high as 15, in which case the number of bivalents would be only 3. In such a cell the band of lagging univalents might be at least as wide as the groups of bivalents. Judging by the number of cells with restituted nuclei at different stages the slenderer bridges usually broke. The new wall commonly began to form across a portion only of the diameter of the cell and later disappeared in cases of complete restitution. A proportion of the very young pollen grains were in triads instead of the usual tetrads.



FIGURES 1 to 8.—*T. durum*×*T. monococcum* F_1. (1) Metaphase and early anaphase of homotypic division. (2) Telophase bivalents, lagging univalents. (3) Chromosomes scattering without division. (4) Partially incorporated univalents. (5 and 6) Slender and stouter bridges formed from univalents. (7 and 8) Restituted nuclei. All figures are from smear preparations, were made with camera lucida, Zeiss apochromatic objective ×40, eyepiece×20, and were reduced to a magnification of about 1500.

As a result of the restitution gametes with 21 chromosomes (the sum of the numbers in the parental gametes) would be formed. If 7 pairs had conjugated in the prophases of the heterotypic division, the interphase nuclei would have 7 halves of bivalents and 7 halves of univalents, and the restituted pollen grain would have 7+7 from bivalents and 7 from univalents, making 21 in all. If 6 pairs had conjugated it would have $6+6+9=21$; if 5 pairs, $5+5+11=21$.

Several cases of the production of gametes with somatic chromosome number have been reported. These have resulted from the doubling of the chromosomes in somatic tissues or from a process of restitution following the heterotypic division as first described by ROSENBERG (1927). HÅKANSSON (1929) has recently reported the production of diploid gametes in Salix through an irregularity at the homotypic division, but his case apparently involves the fusion of the 2 homotypic spindles. In wheat this could not occur because a wall invariably separates the interphase nuclei. Our case is much more like that of ROSENBERG but restitution follows the homotypic division instead of the heterotypic as in his case.

Whether the restitution follows the heterotypic or the homotypic division seems to depend on the comparative degree of irregularity and in particular on the behavior of the univalents. Although these lag behind the bivalents in wheat, they divide in a very regular fashion at the first division, and move in an orderly line to join the bivalents, always arriving at the pole in time to become incorporated in the new nucleus. At the second division, on the other hand, since they fail to divide, they lag for a much longer time, move slowly and irregularly toward the ends, and become much elongated. All these conditions favor restitution of a single nucleus from the whole mass.

Although the number of chromosomes in the gametes would be the same when restitution follows the second as when it follows the first division, the constitution of the chromosomes might be quite different. For example, if 7 pairs had conjugated, restitution after the first division would always give 7 *monococcum* and 14 *durum* chromosomes, but after the homotypic it might give gametes with from 0 to 14 *monococcum* chromosomes, plus enough *durum* ones to make 21. If the interphase nucleus received the 7 *monococcum* halves of the bivalents, the restituted nucleus would have 2×7 *monococcum* chromosomes plus the 7 *durum* ones which never mate. If the interphase nucleus received no *monococcum* halves of the bivalents the restituted nucleus would have 2×7 *durum* chromosomes from bivalents, plus the 7 *durum* ones which never mate.

The only special process observed which tended to increase the proportion of 14-chromosome gametes was an occasional failure to form a plate at the second division. In these cases all the chromosomes failed to divide and simply scattered toward the poles (figure 3). Such cases were easy to distinguish from the usual anaphase by the number, size, and form of the chromosomes. At the usual type of division the chromosome plate extended almost completely across the cell (figure 1), whereas in cases of scattering the group was long and narrow. The scattering without division was favored by the elongated form of many interphase nuclei. This form was apparently due to the incorporation of tardy univalents which had been near the outside of the cell at the heterotypic division and consequently were late and joined the edge of the daughter nucleus.

In such cases of scattering the conditions were favorable for restitution. But by the time it had occurred it was impossible to decide whether the division had been by scattering or of the usual type. If restitution should occur following scattering the new nucleus would have about 14 chromosomes (7 halves of bivalents plus 7 halves of univalents, or 6+9, etc.). In this way the proportion of gametes with approximately 14 chromosomes would be increased.

CHROMOSOMES IN F$_3$

Table 6 gives the chromosome numbers of the F$_3$ plants which have been examined. The single plant with 26 was the offspring of a 28-chromosome F$_2$ in which at least 2 pairs usually failed to conjugate. The single 35-chromosome offspring of 29-chromosome F$_2$ was probably the result of natural cross-pollination by *vulgare.*

TABLE 6

Somatic chromosome numbers in F$_3$.

F$_2$	F$_3$																
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
28	1	..	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..
29	..	1	5	3	..	..	..	..	..	1	..	..	..	..	..	..	..
30	..	..	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..
35	..	..	4	1	1	..	2	..	1	..	..	..	..	..	..	1	..
36	..	..	..	..	..	..	..	..	..	2	..	1	1	3	1	..	1
42	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3

In general the chromosome behavior in F$_3$ was much more regular than in F$_2$. For example, in each of the 11 plants with 28 chromosomes which were the offspring of F$_2$ with the same number, the mother cells usually showed no univalents; in some of them none were ever seen; in others a few were occasionally observed.

All but 1 of the offspring of 35-chromosome plants had a smaller number, and in future generations would apparently be reduced to the 28-chromosome condition. The offspring of 36-chromosome plants, on the other hand tended toward the 42-chromosome condition. The 3 offspring of 42-chromosome F_2 all had 42 chromosomes and showed only occasional non-conjunction in 1 or 2 pairs.

EXTERNAL CHARACTERS

Owing to the small number of plants, the very large amount of pollen abortion, and the occurrence of some out-crossing, little would be gained by an attempt to analyze the inheritance of the individual characters. Nevertheless, in view of the chromosome situation it appears desirable to record the general genetic results.

The condition of the more prominent contrasting characters in the parental species and in F_1 is shown in table 7. The figures given in connection with spike density are averages obtained by dividing the length of the spike in millimeters by the number of spikelets; those in connection with

TABLE 7

CHARACTER	*durum*	*monococcum*	F_1
Stem	Solid	Hollow	Solid
Spike density	Dense (3.0)	Very dense (2.0)	Near *durum*
Spikelet form	Narrow (1.5)	Very narrow (2.3)	Near *monococcum*
Empty glume			
Second tooth	Small	Prominent	Near *monococcum*
Rib	Absent or slight	Prominent	Intermediate
Ratio flowering glume to empty glume	$\frac{1}{4}$ or less longer	$\frac{1}{3}$ or more longer	Near *monococcum*
Palea	Not split	Split	Not split
Rachis			
Toughness	Tough	Very brittle	Brittle
Width	Narrow	Wide	Intermediate
Hairs	None below or few	Full length	Near *durum*
Basal hairs	Medium tuft	Large tuft	Medium tuft
Grain			
Flatness	Slight	Pronounced	Slight
Furrow	Deep	Slight	Near *durum*

spikelet form by dividing its length by its breadth. In regard to 7 of the 13 pairs of characters the *durum* condition is partially or completely dominant; in regard to 3 the *monococcum* condition is partially dominant. *Turgidum* is like *durum* in regard to most of these characters, although its contrast with *monococcum* is less in regard to some and greater in regard to others.

The *monococcum* condition of every character except density of spike was recovered among 50 F_2 *durum*×*monococcum*, including those studied cytologically. The hollow stem and indistinct furrow on the grain characteristic of *monococcum* appeared in about 1/15 of the plants (excluding out-crosses with *vulgare*); the long, narrow spikelets, split palea, extremely flat grains, prominent rib on empty glume, and large tuft of hairs at the base of the spikelet in from 1/5 to 1/8; the prominent secondary tooth of the empty glume, the brittle and the broad rachis as well as the full fringe of hairs on the rachis, in 1/3 to 1/5; the long flowering glume in nearly 1/2.

In view of the facts that only 4 of the plants examined cytologically had fewer chromosomes than the *durum* parent, that those 4 had only 1 or 2 fewer, and that the *durum* condition of the majority of characters was partially dominant in F_1, the large proportion of plants with individual *monococcum* characters is important. At the most only half the chromosomes could be from *monococcum*, usually only one-quarter, and often less. Seven of the 14 pairs present in most F_2 could include no *monococcum* chromosome. These considerations indicated that the distinctively emmer characters must be carried chiefly in the 7 chromosomes which pair with those of *monococcum*, whereas from emmer-*vulgare* crosses it has been concluded that the distinctively *vulgare* characters are carried in the extra 7 chromosomes which do not pair with those of emmers.

In crosses between emmer and *vulgare* the contrasting characters are associated in a body, nearly all being either present or absent in individual F_2. In our emmer-*monococcum* hybrids that was not the case. Many different combinations of *durum* and *monococcum* characters occurred.

A striking feature of the F_2 was the appearance of conditions not present in either parent and not intermediate between the conditions of the parents. For example, several plants had no beards. That they could not have been natural crosses with *vulgare* was shown by their other characters as well as by their chromosome numbers; and there were no beardless plants, other than *vulgare* types with which the F_1 might have crossed. Possibly the genes for beards in the two parents are in different chromosomes which do not mate with each other; in that case an F_2 plant might lack genes for beards entirely. Or an inhibiting factor which had been suppressed in one of the parents might have been freed from its suppressor. Other examples of such new conditions were a secondary tooth of the empty glume more pronounced even than in *monococcum*, and the entire absence of rachis hairs and of the basal tuft.

SUMMARY

Crosses between emmer wheats (n = 14) and *monococcum* (n = 7) have been studied cytologically in the second and third generations.

In F_2 no plant had fewer than 26 somatic chromosomes; the great majority had from 27 to 30, approximately the number in one parent; a few had 35 and 42. There was much non-conjunction; the amount varied widely in the mother cells of the same plant and expecially from plant to plant.

F_1 gametes with fewer than 13 chromosomes did not function. The successful gametes had approximately 14 or 21.

Restitution of a single nucleus following the homotypic division sometimes occurred. This was due to the presence of a wide bridge formed from lagging univalents and connecting the groups at the poles. Restituted nuclei had 21 chromosomes, the sum of the gametic numbers of the parents. The proportion of 14-chromosome gametes may have been increased by restitution following homotypic divisions in which the chromosomes scattered without dividing.

A hexaploid wheat has been produced by crossing a tetraploid and a diploid. Its characters are not those of common hexaploids.

In spite of the absence of segregates with chromosome numbers approaching that of *monococcum*, each *monococcum* character appeared in a considerable proportion of F_2. The emmer characters are carried chiefly in the 7 chromosomes which pair with those of *monococcum*.

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