

CHROMOSOME NUMBERS IN FUNCTIONING GERM CELLS OF SPECIES-HYBRIDS IN WHEAT¹

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INTRODUCTION

The second and later generations of hybrids between tetraploid and hexaploid species of wheat have chromosome conditions which are very different from those which are to be expected on the basis of the numbers in F₁ gametes. The parental numbers appear far too frequently in F₂, and the intermediate numbers disappear in later generations. The reasons for these differences from the expected cannot be satisfactorily determined by the study of ordinary hybrids alone. But additional information, particularly in regard to the chromosome numbers of those gametes which are capable of functioning, can be obtained from the study of backcrosses.

KIHARA (1919, 1924) and SAX (1922a) have shown that in the F₁ the 14 chromosomes from the tetraploid parent (emmer series) mate with 14 from the hexaploid parent (*vulgare* series), leaving 7 from the latter unmated. These 7 univalents fail to divide at the homotypic division and move at random to either pole. The chromosome numbers of the gametes therefore vary between 14 and 21, and the frequencies of the various numbers should be 1, 7, 21, 35, 35, 21, 7, 1. Consequently the great majority of plants in F₂ and in later generations should have intermediate numbers.

But several authors have shown that segregates with 28 and 42 chromosomes (somatic) are numerous, that many others have 29, 30, 40 or 41,

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and that the proportion of plants with approximately 35 is very small in comparison with expectations (KIHARA 1921, 1924; SAX 1923; THOMPSON 1925; THOMPSON and HOLLINGSHEAD 1927). Furthermore those intermediate numbers which were present in F_2 were shown to disappear in later generations. In addition KIHARA (1924) found that the chromosome formula of plants with more than 14 bivalents must be written $(14+x)$ bivalents $+(7-x)$ univalents. If any plant has more than 14 bivalents it has also enough univalents to make the total number 21. Such combinations as 15 bivalents plus 0 to 5 univalents, 16 plus 0 to 4, etc., do not appear, or only very rarely, although they should be expected fairly frequently, particularly in certain F_3 progenies.

Different suggestions were made by the authors mentioned to account for these results. SAX thought that they were due to the failure of the intermediate classes of gametes to function owing to chromosome unbalance. KIHARA attributed them rather to the failure of certain classes of zygotes to develop. There are other possible factors such as the loss of univalent chromosomes through lagging, chromosome conditions in the endosperm, some peculiar method of chromosome distribution, or some favorable relationship between chromosome numbers in male and female cells.

In order to decide the exact cause, it is necessary to know the chromosome constitution of the gametes which are capable of functioning. By means of counts in F_2 , it is possible to determine the total number in the 2 gametes which unite to produce an F_2 plant but not the number in individual gametes. But by using backcross material this information can be obtained. When the chromosome number of the backcross has been determined, and that of the pure parent is known, that of the F_1 gamete which functioned can easily be inferred.

KIHARA (1925) has reported some results of backcrossing *T. Spelta* \times *T. polonicum* F_1 male with the pure parents. Of the backcross with *polonicum* 4 plants were examined and all were shown to have resulted from the functioning of F_1 male gametes with 14 chromosomes. Of the backcross with *Spelta*, 10 plants were examined and 8 were shown to have resulted from the functioning of F_1 male gametes with 19 to 21 chromosomes. Since *polonicum* has 14 and *Spelta* 21, KIHARA concluded that the pollen grains which function are those which have a chromosome number similar to that of the female. It is possible, for example, that a 14-chromosome pollen tube may not develop as well as a 21-chromosome tube in a stigma of a plant with 21 chromosomes.

WATKINS (1927) has reported counts on backcrosses with *turgidum* \times

vulgare which lead him to conclude that all F_1 female gametes are capable of functioning, but that there is much elimination of male gametes.

METHODS

All chromosome counts were made on pollen mother-cells of stamens fixed in a mixture of absolute alcohol and acetic acid (2:1) and examined in aceto-carmin. Such preparations are much better than paraffin sections for the study of univalents, though usually not for total counts if the numbers are large. In this case the determination of the number of univalents is all that is necessary since if the backcross is with the 14-chromosome parent the number of univalents is the same as in the F_1 gamete which functioned (all 14 from the pure parent mating with 14 from the F_1 gamete); and if the backcross is with the 21-chromosome parent, the number of univalents is 7 minus the number in the F_1 gamete (each univalent from the latter finding a mate among the extra 7 chromosomes from the *vulgare* parent). Nevertheless, whenever it was possible—and this was the case in nearly every plant—the total number of bivalents and univalents was also determined for confirmation.

The number of univalents can be determined most easily and accurately at the heterotypic anaphase since they lag behind the bivalents, and since in aceto-carmin preparations of fixed material, side views are usually obtained. The number visible in the different pollen mother-cells of the same plant varies somewhat owing to premature splitting, failure to move into the equatorial position, or entanglement with the bivalents. But when any considerable number of cells is available for observation the true number appears in a large proportion of cases, as can easily be confirmed from total counts. At heterotypic metaphase, although most of the univalents are off the plate and can be recognized, some of them may be at the edge so that accurate determination of them is more difficult than at anaphase, though usually not impossible. In a few cases a small proportion of the cells showed 1 or 2 univalents more than was definitely determined to be the true number. This was apparently due to the occasional failure of 1 of the primary 14 pairs to mate. Many of the counts were made on material raised in the greenhouse during the winter of 1926–27, and the rest on material raised in the field in 1927.

Four kinds of F_1 plants were used: *dicoccum-vulgare* 1, *durum-vulgare* 1, *durum-vulgare* 2, and *dicoccoides-vulgare* 1. *Vulgare* 1 is the variety Marquis; *vulgare* 2 is of Chinese origin; the *dicoccum* variety is a white spring emmer; the *durum* is Iumillo; the *dicoccoides* is wild emmer. The *vulgares* have 21 chromosomes and each of the others 14.

EXPERIMENTAL DATA

Table 1 gives the cytological findings for a number of kinds of back crosses. It shows the frequencies of the F_1 gametes, with the various numbers of univalents, which functioned to produce the backcrosses. The total number of chromosomes in these gametes is obtained by adding 14 (the bivalents) to the numbers 0 to 7 in the first line of the table. Both male and female gametes of each of the 4 kinds of F_1 were investigated by using F_1 as both pollen and seed parent in the backcrossing. Also in the case of the *durum-vulgare* F_1 , backcrosses were made with both *durum* and *vulgare* parents. The data on the F_1 gametes which functioned in all these kinds of backcrosses are given in the table.

In the backcrosses with *vulgare*, the number of univalents actually seen in each case was 7 minus the number shown, since each univalent in the F_1 gamete would mate with one of the 7 extra chromosomes from the *vulgare* parent and the rest of the 7 would be left unmated.

A study of table 1 brings out certain conclusions which may now be discussed in order.

TABLE 1

Frequencies of functioning F_1 gametes with various numbers of univalent chromosomes.

BACKCROSS	UNIVALENTS IN F_1 GAMETES								TOTALS
	0	1	2	3	4	5	6	7	
1. <i>Dicoccum</i> ♀ × (<i>vulgare</i> 1- <i>dicoccum</i>) F_1 ♂	18	8	2	3	2	0	2	2	37
2. <i>Dicoccum</i> ♂ × (<i>vulgare</i> 1- <i>dicoccum</i>) F_1 ♀	10	6	5	6	2	0	0	0	29
3. <i>Durum</i> ♀ × (<i>vulgare</i> 1- <i>durum</i>) F_1 ♂	12	7	4	2	0	0	1	3	29
4. <i>Durum</i> ♂ × (<i>vulgare</i> 1- <i>durum</i>) F_1 ♀	14	3	4	2	4	2	1	2	32
5. <i>Durum</i> ♀ × (<i>vulgare</i> 2- <i>durum</i>) F_1 ♂	3	2	0	1	2	2	0	5	15
6. <i>Durum</i> ♂ × (<i>vulgare</i> 2- <i>durum</i>) F_1 ♀	1	1	3	6	4	2	2	1	20
7. <i>Vulgare</i> 1 ♀ × (<i>vulgare</i> 1- <i>durum</i>) F_1 ♂	8	4	2	1	1	1	2	5	24
8. <i>Vulgare</i> 1 ♂ × (<i>vulgare</i> 1- <i>durum</i>) F_1 ♀	5	2	3	2	2	3	0	0	17
9. <i>Vulgare</i> 1 ♀ × (<i>vulgare</i> 1- <i>dicoccoides</i>) F_1 ♂	2	1	2	1	0	1	1	1	9
10. <i>Vulgare</i> 1 ♂ × (<i>vulgare</i> 1- <i>dicoccoides</i>) F_1 ♀	2	1	1	2	1	1	0	0	8
11. <i>Vulgare</i> 2 ♂ × (<i>vulgare</i> 2- <i>durum</i>) F_1 ♀	0	0	2	2	3	1	0	1	9
<i>Expected proportions</i>	1	7	21	35	35	21	7	1	

THE FAILURE TO FUNCTION OF MANY GAMETES WITH
INTERMEDIATE CHROMOSOME NUMBERS

The last line of the table shows the proportions of the various classes of gametes which are to be expected if all are capable of functioning. The actual proportions are very different in every case. The most conspicuous difference is the small number of gametes with intermediate numbers (3, 4, and 5). For example, the ratio of gametes with 0 to those with 3 is expected to be 1:35, whereas it is actually 18:3, 10:6, 12:2, etc. A result of this kind would be anticipated from the work of several investigators on F_2 . SAX (1923) believes that nearly all F_1 gametes with intermediate numbers are sterile. KIHARA (1924), on the other hand, thinks they are all capable of functioning but that their failure to produce offspring is due to zygotic mortality. These results strongly favor the theory of gametic sterility. Nevertheless a high enough proportion of them is capable of functioning to produce many F_2 plants. Presumably their usual failure to function is due to the bad effects of an unbalanced chromosome number. Whether they actually die or are merely unsuccessful in competition with the others is not determined. The percentage of visibly abortive pollen in F_1 is not high enough to account for these figures.

In a later publication (1925) KIHARA reported data which indicated that the functioning of the pollen grain may depend on the relation of its chromosome number to that of the female plant. When *Spelta* × *polonicum* F_1 male was backcrossed with *polonicum* female, all the 4 F_1 pollen grains which functioned to produce the plants examined, had 14 chromosomes; but when the backcross was with *Spelta* 8 of the 10 grains which functioned had from 19 to 21 chromosomes. KIHARA concluded that the pollen grains which function are those which have a chromosome number similar to that of the female. Failure to function may result from poor growth of the pollen tube in a stigma which is unsuitable because of its chromosomes.

Our results do not support this conclusion. In the backcross with *durum* female (line 3 of table 1) 19 out of 29 grains had 14 or 15 chromosomes and 4 had 20 or 21; in the backcross with *vulgare* female (line 7) 12 out of 24 grains had 14 or 15 and 7 had 20 or 21. Grains with the higher numbers were, therefore, only slightly more successful on *vulgare* than on *durum* stigmas. Half the grains which were successful in the *vulgare* backcross had only 14 or 15 chromosomes.

PREPONDERANCE OF 14- OVER 21-CHROMOSOME GAMETES

Chromosome unbalance will not account for the great preponderance, in nearly every case, of gametes with no univalents, or only 1, over those

with 6 or 7. It will be observed from the table that the ratio of gametes with 0 univalents to those with 7 in the different cases is 18:2, 10:0, 12:3, etc., whereas it should be 1:1. This is doubtless due, in part at least, to the loss of chromosomes through lagging at the reduction divisions. These laggards frequently fail to become incorporated in the new nucleus and degenerate in the cytoplasm. (For the frequency of this phenomenon see THOMPSON and HOLLINGSHEAD 1927). Intermediate numbers would thus tend to become low, and high numbers to become intermediate (a condition which rarely functions). Whether this is the correct explanation or not, there are certainly far more functional gametes with 14 than with 21 chromosomes. This results in the great preponderance of emmer types in F_2 noted by THOMPSON and HOLLINGSHEAD in *dicoccum-vulgare* and to a less extent by THOMPSON (1925) in *durum-vulgare* hybrids.

One exception to this rule should be noted. When *vulgare 2* is used in making *durum-vulgare* crosses, the F_1 gametes with 7 univalents are as numerous as those with 0 or more numerous.

DIFFERENCES BETWEEN MALE AND FEMALE GAMETES

Another important point evident in the table is that male gametes with intermediate numbers are eliminated in greater proportions than are female gametes with the same numbers. In nearly every case there is a smaller proportion with intermediate numbers when the F_1 is the male parent than when it is the female parent. This may be due to the greater competition among the numerous male gametes, only the stronger ones usually functioning. In no case, however, are all the males with intermediate numbers eliminated. And in no case are all the female gametes functional. In every case in which the F_1 was the female parent, the proportions of gametes with intermediate numbers are less than the theoretical. The only case in which the expected numbers are approached is where *vulgare 2* was one parent.

This result is quite different from that obtained by WATKINS (1927) with *vulgare* × *turgidum* hybrids. He is of the opinion that all female F_1 gametes in that cross are capable of functioning. The correctness of our conclusion, for our material at least, is confirmed by comparing the percentage of seed set in backcrossing where the F_1 was the female parent, with that set in straight crossing. The figures in this connection are given in table 2. In every case the percentage of seed set is considerably less in the backcross, showing that a higher proportion of the eggs of F_1 than of the pure parent fails to function. These crosses were all made in the same year by the same person.

TABLE 2
Percentages of pollinated flowers setting seed.

<i>Vulgare-durum</i> F ₁ ♀ × <i>durum</i> ♂	34.46
<i>Vulgare-durum</i> F ₁ ♀ × <i>vulgare</i> ♂	33.96
<i>Vulgare-dicoccum</i> F ₁ ♀ × <i>dicoccum</i> ♂	33.40
<i>Vulgare-dicoccum</i> F ₁ ♀ × <i>vulgare</i> ♂	34.44
<i>Vulgare</i> ♀ × <i>durum</i> ♂	72.87
<i>Vulgare</i> ♀ × <i>dicoccoides</i> ♂	59.21
<i>Dicoccum</i> ♀ × <i>vulgare</i> ♂	84.33

DIFFERENCES AMONG THE KINDS OF CROSSES

It is also evident from table 1 that somewhat different results are obtained with different kinds of F₁. For example there is a greater elimination of intermediate numbers in *vulgare-dicoccum* than in other F₁'s. When *vulgare 2* is used in crossing with *durum* the results are very different from those obtained when *vulgare 1* is used. In the former case there is much less elimination of intermediate numbers. Its female gametes (backcrosses number 6 and 11) approach the expected much more closely than any of the others and both male and female gametes have 6 or 7 univalents much more frequently than do those of other crosses. Not only the kind of F₁ but also the kind of backcross is important. The elimination of both intermediate and high numbers of univalents is less when the backcross is made to *vulgare* than when it is made to *durum*. All these differences emphasize the danger in drawing sweeping conclusions from work with a limited variety of material. In the difficult problems of practical breeding with wheat, what is found to be impossible to accomplish with one or several crosses, may prove quite feasible with others.

CHROMOSOME NUMBERS IN RELATION TO ENDOSPERM DEVELOPMENT AND SEED MORTALITY

Certain aspects of these results have been determined or influenced by differences in the germinating capacity of different classes of seeds. This is illustrated in table 3 which shows the percentages of germination of grains from certain reciprocal backcrosses as well as from straight crosses. The grains recorded are those produced directly on the plants which were artificially pollinated, not on their offspring. It is clear from these data that in backcrosses with the 14-chromosome parent the germination is better, in some cases much better, when the F₁ is the female, than when it is the male parent. Even in straight crosses there is a

marked difference in germination depending on the direction of the cross. If the 21-chromosome parent is the female the germination is much higher than if it is male.

TABLE 3
Comparative germination in reciprocal crosses and backcrosses.

	PLANTED	GERMINATED	PERCENT GERMINATED
<i>Dicoccum</i> ♀ × F_1 ♂	72	48	66.6
<i>Dicoccum</i> ♂ × F_1 ♀	67	52	77.6
<i>Durum</i> ♀ × F_1 ♂	40	21	47.5
<i>Durum</i> ♀ × F_1 ♀	31	28	90.4
<i>Vulgare</i> ♀ × F_1 (<i>vulgare-durum</i>) ♂	29	26	89.6
<i>Vulgare</i> ♂ × F_1 (<i>vulgare-durum</i>) ♀	38	23	60.5
<i>Vulgare</i> ♀ × F_1 (<i>vulgare-dicoccoides</i>) ♂	17	17	100.0
<i>Vulgare</i> ♂ × F_1 (<i>vulgare-dicoccoides</i>) ♀	22	12	54.5
<i>Durum</i> ♀ × <i>vulgare</i> ♂	93	51	55.9
<i>Durum</i> ♂ × <i>vulgare</i> ♀	19	16	84.2
<i>Dicoccum</i> ♂ × <i>vulgare</i> ♀	10	8	80.0
<i>Durum</i> ♀ × <i>Spelta</i> ♂	24	8	33.3

Note: These data are for directly crossed seeds, not for seeds borne on plants resulting from crossing. The seeds recorded in the first 4 sections of the table would produce backcross plants; those in the last 2 sections would produce F_1 .

These differences in germination depend directly on the different degrees of endosperm development which are evident from the varying amounts of shrivelling of the seeds. And the endosperm development depends on chromosome conditions, as has been pointed out by WATKINS (1927). The chromosome number in the endosperm of seeds resulting from crossing a 21- with a 14-chromosome wheat will depend on the direction in which the cross is made. If the 21-chromosome plant is the female, the endosperm will have $56(21 \times 2 + 14)$ chromosomes since it is formed from the fusion of 2 female nuclei (each with 21) and a male nucleus (with 14). But if the 21-chromosome plant is the male, the endosperm will have $49(14 \times 2 + 21)$. In the one case the extra 7 *vulgare* chromosomes are diploid and in the other haploid. From the data on straight crosses given in table 3, it is clear that germination is much better when the 7 are diploid. Similar considerations must be kept in mind in discussing F_1 and plants which may have between 14 and 21 chromosomes.

TABLE 4
Chromosome numbers and endosperm development.

		LARGE PUMP	SMALL PUMP	LARGE WRINKLED	SMALL WRINKLED	SHRIVELLED	TOTALS
<i>Vulgare</i> 1 ♀ × <i>Vulgare</i> 1- <i>durum</i> F ₁ ♂	Frequency Planted	32	48		10	7	97
	Died Univalents in F ₁ gametes	10 2 7, 7, 7, 7, 6, 6, 5	17 1 4, 3, 2, 2, 1, 1, 1, 0, 0, 0, 0, 0,		2 0 1, 0		29 3
<i>Vulgare</i> 1 ♂ × <i>Vulgare</i> 1- <i>durum</i> F ₁ ♀	Frequency Planted	11	2	44	12	20	89
	Died Univalents in F ₁ gametes	8 0 2, 3, 4, 4, 5, 5	2 1	23 10 0, 0, 0, 0, 0, 1, 2, 2, 2, 3, 4	5 4		38 15
<i>Vulgare</i> 2 ♂ × <i>Vulgare</i> 2- <i>durum</i> F ₁ ♀	Frequency Planted	8	5	26	16	21	76
	Died Univalents	7 0 3, 4, 5, 5, 7	5 0 4, 4	10 6 2, 2	3 3		23 9
<i>Vulgare</i> ♀ × <i>Vulgare-dicoccoides</i> ♂	Frequency Planted	10	14				24
	Died Univalents	8 0 3, 4, 5, 6, 7	9 0 0, 0, 1, 2				17 0
<i>Vulgare</i> ♂ × <i>Vulgare-dicoccoides</i> ♀	Frequency Planted	1		15		15	31
	Died Univalents	1 0		14 4 0, 0, 3, 3, 4, 5		7 4 1, 2	22 8
<i>Durum</i> ♂ × <i>Vulgare-durum</i> ♀	Frequency Planted	24	15				39
	Died Univalents	8 0 0, 0, 1, 2, 6	3 0 4, 4				11 0

Information regarding the interrelationships between chromosome numbers, the direction of crossing, endosperm development, and germination is given in table 4. If one compares the first two sections of the table, it is seen that in backcrossing with the 21-chromosome parent, the proportion of wrinkled and shrivelled seeds obtained is low when the F_1 is the male parent but very high when F_1 is the female. In the former case (*vulgare* ♀ × F_1 ♂) the endosperm has the extra 7 diploid plus whatever number of univalents the male contributes, which is usually 0 or 7. And such endosperm is almost always well developed. Therefore the endosperm develops well if the 7 are exactly diploid or triploid or nearly so. From the chromosome numbers determined (bottom of first section of table 4) it is also evident that the triploid condition gives better endosperm than the diploid, since when the male contributes 6 or 7 univalents the seeds are large, whereas when it contributes 0, 1 or 2, they are small (though not shrivelled).

In the reciprocal of this cross (F_1 ♀ × *vulgare* ♂; second section of the table) the endosperm contains in the diploid condition whatever chromosomes are contributed by the F_1 (usually less than 7) plus the complete set of 7 contributed by the *vulgare* male. Consequently the endosperm is usually haploid for all 7 (when F_1 contributes 0 univalents) and frequently triploid with respect to some chromosomes and haploid with respect to the rest. Under these conditions endosperm development and germination is usually poor. Moreover the actual chromosome counts (bottom of second and third sections) show that the small proportion of round seeds do have the triploid condition of most of the chromosomes while the wrinkled ones have the haploid.

A similar situation is seen in the backcross of *vulgare-dicoccoides* with *vulgare*.

When the F_1 is backcrossed with the *durum* the seeds are plump. In this case the extra 7 *vulgare* chromosomes are rarely represented at all in the endosperm, since the F_1 usually contributes none, and of course the *durum* has none. Therefore the endosperm is like that of pure *durum*.

All these cases are in line with a general rule which may be stated as follows: The endosperm is well developed when it is (a) entirely without the extra 7 *vulgare* chromosomes, (b) when it has either 2, or, (c) better still 3 complete sets. It is likely to be badly developed when it is (a) haploid for all 7 or (b) diploid or triploid for some only of the 7 or (c) diploid or triploid for some and haploid for others. In general the endosperm appears to be affected in the same way as the gametes by unbalanced chromosome numbers; the unbalance may be even greater in the endosperm.

A number of important applications of these conclusions may be pointed out. In ordinary crossing one obtains many more F_1 plants for the same amount of labor if *vulgare* is the female than if it is the male parent, since in the latter case the endosperm is haploid with respect to the seven. This is important in practical breeding where a large F_2 may be required. Again it is well known that certain wide crosses, for example wheat \times rye, wheat \times *Aegilops*, *vulgare* \times *monococcum*, etc., can be made in only one direction. The species with the larger chromosome number must be used as the female, in order to give an endosperm which is diploid for the extra chromosomes.

The conclusions reached above make it probable also that the F_2 and later generations usually raised are not fair samples. There is a tendency to select the better looking seeds for planting and to leave the shrivelled ones or to take no special care with them. But the embryos of the better seeds are likely to have either 0 or all 7 of the extra chromosomes while the shrivelled ones are likely to have the intermediate numbers. It is therefore probable that the lack of intermediate chromosome numbers is due in part to the conscious or unconscious selection of the better seeds for planting. Of course a proportion of the poor seeds would fail to germinate in any case, particularly if conditions were not favorable. Nevertheless the frequency of plants with intermediate chromosome numbers would be increased by giving special attention to the poorer seeds. And it is probable that such plants are the ones most likely to possess the combinations of characters which the practical breeder desires.

SAX (1922b) has reported some results which are in agreement with this conclusion. In a cross between Kubanka and Bluestem he found that a majority of F_2 seeds (borne on F_1 plants) which failed to germinate were in the lower weight classes. He also found a correlation of 0.24 between wrinkling of F_2 seeds (borne on F_1) and sterility of F_2 plants which produced heads. He could find no correlation, however, between wrinkling and size of F_2 plants.

It is probable that the frequency of intermediate numbers in table 1 would have been increased by selection of wrinkled seeds and special care in their germination. These facts about the effect of chromosome numbers in endosperm development and germination were not realized when the seeds of some of the backcrosses were planted. In some cases, however, all the seeds available were planted, but no special care was taken with the shrivelled ones.

BEARING ON RESULTS PREVIOUSLY REPORTED FOR F_2
AND LATER GENERATIONS

The chromosome numbers in F_2 and later generations as reported by SAX (1923), KIHARA (1924), THOMPSON (1925), THOMPSON and HOLLINGSHEAD (1927), are in general such as would be expected if the F_1 gametes which are capable of functioning have the chromosome numbers reported in this paper. One discrepancy is a frequency of plants with intermediate numbers lower even than our figures would indicate. This may be explained in part by the selection of the better seeds for planting. It may also be due in part to the greater effect of chromosome unbalance in the endosperm in the ordinary hybrids than in the backcrosses. In the latter one parent contributes 1 or 2 complete sets of the 7 or none at all, whereas in the former the F_1 makes all 3 contributions of intermediate numbers to the endosperm. The effect of chromosome unbalance is therefore likely to be greater in the endosperm of ordinary hybrids than in that of backcrosses.

Another marked discrepancy is the absence from F_2 of any plants with more than 14 bivalents and less than 21 as the sum of bivalents and univalents. Such combinations as 15 bivalents plus 0–5 univalents, 16 plus 0–4, etc., do not appear or only very rarely. They should be found if the gametes have the numbers shown in table 1. They should not be very frequent in F_2 but they should occur, and they should be fairly frequent in certain F_3 families. This study shows that their absence is not due entirely to gametic elimination. It must be due also to zygotic mortality. Apparently zygotes having more than 14 bivalents without having enough univalents to make the total 21 are not viable. They may die as a result of endosperm abortion. They could result only if both gametes had an intermediate number of univalents. Therefore the endosperm could not be triploid or even diploid for all 7 but would be triploid for some of the 7. For example if the pollen grain had chromosomes a and b of the extra 7, and the egg had a, b and c, then the endosperm would have 3 a's, 3 b's and 2 c's, and none of the others. It has been shown from the data on backcrosses that such an endosperm would be severely shrunken and the seed probably fail to germinate or die early. Hence the non-appearance of such combinations may be due to endosperm abortion. Of course the young zygotes may die from other causes.

SUMMARY

1. An effort has been made, by the study of backcrosses, to determine the causes of the cytological conditions which have been reported for

hybrids between 14- and 21-chromosome wheats. The study of backcrosses makes possible the exact determination of the chromosome numbers of F_1 gametes which are capable of functioning. This information is not obtainable from the study of ordinary crosses. Four kinds of F_1 were backcrossed reciprocally so that both male and female gametes could be investigated and both 14- and 21-chromosome parents were employed in making the backcrosses.

2. In nearly every case the gametes with numbers of extra *vulgare* chromosomes intermediate between 0 and 7 were in much smaller proportions than were to be expected, if all gametes are capable of functioning.

3. In most cases the gametes with no extra univalent chromosomes (14 in all) were much more numerous than those with 7 (21 in all).

4. There are marked differences between the male and female gametes of F_1 , the latter showing less elimination of intermediate numbers than the former, though by no means all eggs are capable of functioning and a proportion of functioning pollen grains do have intermediate numbers.

5. There are marked differences between the different kinds of hybrids with respect to their functional gametes, and slight differences depending on whether a hybrid was backcrossed with the *vulgare* or with the emmer-type parent. It is dangerous to draw sweeping conclusions from a limited variety of material.

6. The endosperm is likely to be poorly developed (and the seeds shrivelled) unless its extra 7 *vulgare* chromosomes are completely absent, or completely diploid, or completely triploid. The farther it departs from these conditions the greater is the shrivelling. Reciprocal crosses may, therefore, give very different results and wide crosses may be possible in only one direction. Unless special care is taken of the shrivelled seeds in species-crosses a fair sample is not obtained in F_2 since the shrivelled ones contain chromosome combinations not likely to be found in plump ones.

7. If gametes with the frequencies found mate at random, the results should be in general like those which have been reported for F_2 . Discrepancies are seen in the lower frequencies of intermediate numbers and especially in the absence of combinations of more than 14 bivalents with less than enough univalents to make 21 altogether. The absence of these may be due to zygotic weakness but may also be attributed to endosperm abortion.

LITERATURE CITED

- KIHARA, H., 1919 Über cytologische Studien bei einigen Getreidearten I. Species-Bastard des Weizens und Weizen-Roggen Bastard. Bot. Mag. 33: 95-98.

- 1921 Über cytologische Studien bei einigen Getreidearten III. Über die Schwankungen der Chromosomenzahlen bei den Speziesbastarden der Triticum-Arten. Bot. Mag. **35**: 19-44.
- 1924 Cytologische und genetische Studien bei wichtigen Getreidearten mit besondere Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem. Coll. Sci. Kyoto Univ. 200 pp.
- 1925 Weitere Untersuchungen über die pentaploiden Triticum-Bastarde. Jap. Jour. Bot. **2**: 299-304.
- SAX, K., 1922a Sterility in wheat hybrids, II Chromosome behavior in partially sterile hybrids. Genetics **7**: 513-552.
- 1922b Sterility in wheat hybrids, III Endosperm development and F₂ sterility. Genetics **7**: 553-558.
- 1923 The relation between chromosome number, morphological characters, and rust resistance in segregates of partially sterile wheat hybrids. Genetics **8**: 301-321.
- THOMPSON, W. P., 1925 The correlation of characters in hybrids of *Triticum durum* and *T. vulgare*. Genetics **10**: 285-304.
- THOMPSON, W. P., and HOLLINGSHEAD, L., 1927 Preponderance of *dicoccum*-like characters and chromosome numbers in hybrids between *T. dicoccum* and *T. vulgare*. Jour. Genetics **17**: 283-307.
- WATKINS, A. E., 1927 Genetic and cytological studies in wheat. III. Jour. Genetics **18**: 375-396.