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Chromosome Behavior in *Triticum* Hybrids

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(With 14 text-figures)

Cytological studies of the genus *Triticum* have been of much interest to geneticists in many countries because they have been of value in solving certain genetic problems in species hybrids, and have indicated the probable origin of the cultivated wheats. In order to adequately present the cytological work with *Triticum* it will be necessary to include the contributions of Sakamura and Kihara of Japan, Gaines and Aase of USA. Thompson in Canada, Watkins and Percival of England, de Mol of Holland, Tschermak and Bleier of Austria, Nikolaeva of Russia, Malinowski of Poland, and Stolze of Germany.

The cultivated species of wheat can be divided into three groups based on chromosome number, sterility relationships, taxonomic differences, economic value, sereological relationships, and resistance to disease. The Einkorn group (*T. monococcum)*, has 7 pairs of chromosomes, is of little economic value, and in general is more resistant to disease than the other wheat species. The Emmer group (*T. dicoccum*, *T. durum*, *T. polonicum*, and *T. turgidum)* has 14 pairs of chromosomes, is of considerable economic value in certain regions, and is more resistant to disease than the bread wheats. The Vulgare group (*T. vulgare*, *T. spelta*, and *T. compactum)* has 21 pairs of chromosomes, is of greatest economic value and widest distribution, and in general is more susceptible to disease than the other two groups. Crosses between species within each group are interfertile while crosses of species of one group with species of either of the other two groups are partially sterile.

Chromosome behavior in partially sterile species hybrids

Several crosses of *T. monococcum* × *T. turgidum* (Emmer group) have been studied to determine chromosome behavior in relation to

sterility. In these crosses the 7 Einkorn chromosomes pair with 7 of the 14 *turgidum* chromosomes at the reduction division of the F_1 hybrid. In one cross the 7 paired chromosomes divide normally but the 7 singles lag at reduction and usually pass to one pole or the other without dividing. In the second division all chromosomes apparently divide normally so that the microspores presumably receive from 7 to 14 chromosomes. This behavior of the chromosomes is somewhat similar to the behavior of chromosomes in a cross of *Aegilops cylindrica* × *T. vulgare*.

More recently Thompson has described the chromosome behavior in a similar cross of Einkorn × *T. turgidum* in which the 7 single chromosomes lag in the F_1 reduction division but ultimately divide and join the bivalents. The single chromosomes do not divide at the second divison but pass to the poles without dividing. This chromosome behavior is similar to that found in Emmer × Vulgare crosses and is probably more typical than that described above.

In crosses of Emmer × Vulgare wheats one parent contributes 14 chromosomes and the other 21. At the F_1 reduction division there are 14 pairs of chromosomes and 7 singles. The 14 Emmer chromosomes presumably pair with 14 of the Vulgure chromosomes leaving 7 single chromosomes from the Vulgare parent. The division of the paired chromosomes is normal. The single chromosomes lag behind the bivalents and begin to divide as the members of the bivalents approach the poles. There are usually 7 single chromosomes in the first reduction division but occasionally only 5 or 6. The single chromosomes do not always reach the poles and are occasionally not included in the nuclei. In the second division the members of the bivalents divide normally buth te singles pass at random, to one pole or the other without dividing. The lagging singles are occasionally lost in the second division and are not included in the microspore *nucleus*. As a result of this behavior of the chromosomes the microspores contain from 14 to 21 chromosomes — 14 contributed at random from the two parents and from 0 to 7 chromosomes from the Vulgare parent.

The F_1 plants are partially sterile although they are usually more vigorous and larger than the parents. About 20 percent of the F_1 pollen is obviously aborted and about 50 percent of the egg cells do not function in most cases. In a backcross Watkins finds that about 90 percent of the eggs are fertile but only about 10 percent of the pollen grains are functional.

In the F_2 of crosses of Emmer × Vulgare wheats all degrees of sterility are found, ranging from plants which do not pass the rosette stage to those which are as fertile as the parents. If all classes of gametes were capable of functioning most of the F_2 segregates should be intermediate and even if the 14 chromosomes which pair are similar or identical the random distribution of the 7 single chromosomes would prevent the recovering of parental forms except in rare cases. Actually, however, a large proportion of the F_2 and F_3 segregates resemble one parent or the other and only these classes are ultimately obtained in a fertile homozygous condition. In almost all crosses recorded there is an excess of the Emmer type of segregates. In 46 F_2 segregates of a cross of Emmer × Vulgare varieties, 21 resembled the Emmer parent, 13 were intermediate and 12 resembled the Vulgare type. Kihara, Watkins and Thompson have obtained similar results.

A cytological analysis of F_2 segregates has shown a striking association between chromosome number and morphological characters and has been of much value in determining the cause of sterility in these species hybrids. The segregates which resemble the Emmer parent have approximately 14 chromosomes; the Vulgare type of segregates have 21 chromosomes or in some cases 19 or 20 chromosomes, while the more typical intermediate segregates have an intermediate chromosome number. In the F_2 and subsequent generations the only fertile segregates are those which have 14 chromosomes and resemble the Emmer parent or those with 21 chromosomes which resemble the Vulgare parent. All segregates with an intermediate chromosome number are eliminsted, and no strictly intermediate types of segregates are obtained in a fertile homozygous condition. Some fertile segregates are obtained, however, which have most of the typical characters of one parent with one or two typical characters of the other parent, but in general the fertile segregates resemble one parent or the other. Occasionally a 14 chromosome segregate is found to be partially sterile. In most, if not all, cases there is an excess of 14 chromosome segregates.

These genetic and cytological results lead to the conclusion that sterility is primarily due to the absence of a complete diploid set of chromosomes. In F_1 the vegetative development is unusually vigorous with 14 pairs of chromosomes and the 7 single chromosomes, but at the reduction division many gametes are found which have an intermediate chromosome number. Such gametes are presumably less fertile and less viable than those with 14 or 21 chromosomes. In F_2 many

segregates are more sterile than the F_1 plants and often they are so weak that thay do not produce heads. The absence of a complete set of chromosomes apparently inhibits vegetative development as well as resulting in gametic sterility. Since the 14 chromosome segregates resemble the Emmer parent and the 21 chromosome segregates resemble the Vulgare parent it follows that the primary 14 chromosomes which pair are similar in genetic constitution and that the extra 7 chromosomes of the Vulgare wheats determine the characters which differentiate these two groups of wheat species. It is also evident that the typical characters of the Emmer and Vulgare wheats can not readily be combined. This conclusion is supported by the fact that although thousands of segregates of crosses between Emmer and Vulgare wheats have been grown in many different countries there is no evidence that the typical and desirable characters of the parents have ever been combined in a single variety of economic value.

Since all fertile segregates of Emmer × Vulgare crosses have 14 chromosomes and resemble the Emmer parent or have 21 chromosomes and resemble the Vulgare parent, it follows, — (1) that sterility is due primarily to an intermediate chromosome number, (2) that the typical Vulgare characters are usually determined by the extra 7 chromosomes and, (3) that the 14 chromosomes of the Emmer wheats are similar in genetic constitution to the 14 Vulgare chromosomes with which they pair in the F_1 hybrid.

Thompson opposes these conclusions because, (1) certain segregates and varieties possess characteristics of both Emmer and Vulgare wheats, (2) *T. monococcum*, with 7 chromosomes, has several characters typical of the Vulgare wheats, (3) different degrees of sterility exist in different crosses of Emmer × Vulgare wheats, and (4) some 14 chromosome segregates are partially sterile.

In view of these difficulties Thompson suggests that "a viable, properly functioning condition may result only when the chromosomes are mostly from the *durum* parent or mostly from the *vulgare* parent". However the most favorable condition for vegetative development is in the F_1 where the maximum number of chromosomes from each parent are functioning together. If gametes containing only Emmer or only Vulgare chromosomes function, about 1 gamete in a million would be viable while as a matter of fact from 50 to 90 percent of the F_1 egg cells are functional and about 20 percent of the pollen grains are obviously aborted. Chromosome

incompatibility may account for sterility in some cases but it obviously can not account for most of the sterility found in these species hybrids.

The presence of a few Emmer characters in a 21 chromosome segregate or a few Vulgare characters in a 14 chromosome segregate may be due to the substitution of a Vulgare univalent for one of the 14 Emmer chromosomes or possibly due to the occasional presence of such a factor in one of the primary 14 chromosomes of the Vulgare parent. The reason for the occasional sterility of 14 chromosome segregates is not clear, but certainly it can not be due to the mixture of chromosomes from either parent in approximately equal numbers.

In order to determine the relation between chromosome number, sterility and genetics, of hybrids between the Vulgare and Emmer wheats, chromosome counts of back crosses with the parents have been made. Counts were made from both root tips and anthers of the cross Marquis (*T. vulgare*) × Kubanka (*T. durum*) F_1 with Kubanka and the reciprocal back cross. In the cross of F_1 × Kubanka 1186 flowers were pollinated and 489 seeds were obtained; 120 seeds were planted in the greenhouse but only 14 plants were used for chromosome counts in the anthers; 182 seeds were used for root tip counts of which 167 germinated and counts were made from 33 individuals. In the reciprocal cross 602 Kubanka flowers pollinated with F_1 pollen produced 301 seeds. About 70 of these seeds were planted in the greenhouse but only 14 plants were suitable for obtaining chromosome counts. For root tip counts 81 seeds were used of which 67 germinated and counts were obtained from 34 individuals. Since greenhouse conditions were rather unfavorable for vegetative growth these back crosses were also grown in the field during the past summer. One hundred and seventy seeds of F_1 × Kubanka were planted, of which 115 produced plants all of which made good growth and headed. Chromosome counts were obtained from 56 of these plants. The chromosome counts from these crosses are shown in Table I. Root tip counts are from fixed material while the counts from pollen mother cells were all obtained from acetocarmine preparations.

If all classes of F_1 gametes are functional the majority of the back cross segregates should have 14 bivalents and 3 or 4 univalents. Segregates with 14 bivalents or 14 bivalents plus 7 univalents should be obtained rarely but in equal numbers. In all anther counts there were 14 bivalents. The chromosome number of F_1 gametes can be obtained from root tip counts by subtracting 14 from the total chro-

Table 1

Chromosome numbers in segregates of Marquis (*T. vulgare)* reciprocal cross. Grown in the

Number of plants with

	Anther counts — 14 bivalents plus following number of univalents								
Back-cross	0	1	2	3	4	5	6	7	n
$F_1 \times K$ (G. H.)	8	1	3	1	—	—	1	—	14
$F_1 \times K$ (F.)	18	18	8	5	6	—	1	—	56
$K \times F_1$ (G. H.)	9	—	—	1	2	1	—	1	14
$K \times F_1$ (F.)	3	3	2	—	—	—	—	—	8
Total	38	22	13	7	8	1	2	1	92
Theoretical[1]) ..	1	5	14	26	26	14	5	1	92

[1]) Approximate theoretical distribution of chromosome counts of back-cross segregates assuming no selective sterility, selective fertilization, or loss of chromosomes.

mosome number. In anther counts the number of chromosomes in F_1 gametes can also be obtained by adding the number of univalents to 14-assuming of course that there is no chromosome elimination in somatic development.

There is considerable chance for selective elimination of certain classes of gametes even in the F_1 egg cells since only 40 percent of these gametes functioned when pollinated with Kubanka pollen and from 170 seeds planted in the field only 33 percent produced plants which were used for chromosome counts. Thus in the most favorable case we have definite counts of only 13 percent of the F_1 female gametes. The use of 14 chromosome pollen grains should not cause selective fertilization since reciprocal crosses of Emmer × Vulgare weats are about a fertile as crosses within a single species.

In case of Kubanka × F_1 considerable selective fertilization might be expected. Since about 20 percent of the pollen grains are obviously aborted and only about 10 percent are functional, there is considerable opportunity for selective elimination of gametes as well as the opportunity for selective fertilization of the functional gametes. The data

Table 1
× Kubanka (*T. durum*) pollinated with Kubanka (K) and the field (F) and in a greenhouse (G. H.)
indicated chromosome number

Back-cross	Root tip counts — total number of somatic chromosomes								
	28	29	30	31	32	33	34	35	n
$F_1 \times K$ (G. H.)	16	2	6	3	1	2	1	2	33
$F_1 \times K$ (F.)	—	—	—	—	—	—	—	—	—
$K \times F_1$ (G. H.)	20	8	1	1	2	1	—	1	34
$K \times F_1$ (F.)	—	—	—	—	—	—	—	—	—
Total	36	10	7	4	3	3	1	3	67
Theoretical[1])..	½	4	11	18	18	11	4	½	67

presented in Table 1 indicate, however, that there is no more selective elimination of male gametes than of female gametes.

Chromosome counts from root tips should give a true random sample of gametes which function because most seeds germinated and there should be no selective elimination of segregates. Since the root tip counts are similar to pollen mother cell counts in their frequency distribution it appears that the latter counts are a true random sample of functional gametes.

Counts of $F_1 \times$ Kubanka and the reciprocal cross show that both the F_1 egg cells and F_1 male gametes have 14 chromosomes far more frequently than would be expected on the basis of random distribution of the 7 single chromosomes. Segregates with 35 somatic chromosomes would be expected as frequently as those with 28 but only 4 plants with 35 chromosomes were found among the 151 segregates while 71 or almost half of the segregates had only 28 chromosomes in the root tips or 14 pairs of chromosomes at the reduction division. Only 22 segregates or about 15 percent had either 31 or 32 somatic chromosomes although with random distribution of univalents and no seleotive elimination

of gametes more than half of the segregates should have these counts. Even if we assume that gametes with an intermediate chromosome number are the only ones which do not function, selective elimination would not be sufficient to account for the excess of 14 chromosome gametes and paucity of 21 chromosome gametes.

The excess of Emmer types of segregates in crosses of Emmer × Vulgare wheats has been mentioned by a number of investigators. Since such segregates have 14 chromosomes the excess of 14 chromosome segregates seems to be general in these species hybrids. Malinowski has suggested that the excess of these segregates may be due to the loss of univalents in the reduction division of F_1 and subsequent generations. These lost chromosomes can be seen in the cytoplasm of the newly found microspore but they ultimately degenerate and can not be seen at later stages. In fixed material of Marquis × Kubanka 560 lost chromosomes were found in 1562 microspores while in aceto-carmine mounts 103 lost univalents were counted in 176 microspores. Usually only one lost chromosome was found in a microspore but occasionally 2 were present. Such a chromosome loss would of course increase the proportion of gametes with a chromosome number approaching 14 but it would not account for the great excess of such gametes.

All of the various factors which might reduce the chromosome number of F_1 gametes; — loss of univalents, selective elimination of gametes, and possibly selective fertilization, do not seem to be adequate to account for the great excess of 14 chromosome gametes. In the back crosses described above it is possible that univalents are frequently eliminated in early embryonic development except when a complete set of 7 univalents are present. Such behavior would account for the chromosome counts in back cross segregates, but there is at present no cytological evidence to support this theory.

There are many questions in regard to chromosome behavior, sterility, and genetic behavior in hybrids of Emmer × Vulgare wheats that remain unanswered. In general we may conclude, however, that sterility in these wheat species hybrids is primarily due to incomplete sets of chromosomes, that the 14 Emmer chromosomes are essentially similar to the 14 Vulgare chromosomes with which they pair, that the 7 extra Vulgare chromosomes determine most of the typical characters of this group of wheat species, and that the desirable and typical characters of the Emmer and Vulgare wheats can seldom if ever be combined

Cytological studies of *Aegilops* × *Triticum* crosses in relation to the origin of the cultivated wheat species

Percival has suggested that the vulgare wheats have orginated from crosses of the Emmer wheats with *Aegilops ovata* and *Aegilops cylindrica.* This conclusion is based on the fact that these *Aegilops* species possess most of the characters which differentiate the Emmer and Vulgare wheats. The large number of Vulgare varieties and their wide distribution is also attributed to the supposed hybrid origin of this group of wheat species. The following differentiating characters of the Vulgare wheats are found in either *Aegilops ovata* or *A. cylindrica* or both: — (1) Long hairs on ridges of leaves with shorter hairs or none on sides of ridges, (2) Thin walled hollow culms, (3) Tough non-disarticulating rachis, (4) Rounded back of empty glume, (5) Absence of prominent keel on outer glume, (6) Short awns, (7) Large number of culms, (8) Spreading habit of growth resembling that of "winter" wheat, (9) Head wider across the spikelet, (10) Glume broad at apex, (11) Soft grain, and (12) Susceptibility to rust. These characters are not always confined to the Vulgare wheats but in general they are not found in species of the Emmer group.

The relationship between *Aegilops* and *Triticum* has been of interest since Requiem discovered a wheat-like plant in France which he called *Aegilops triticoides.* Fabre found that *Aegilops triticoides* developed from seeds of *Aegilops ovata*, which he considered as the progenitor of common wheat. Godron also found *Aegilops triticoides* growing from seeds of *Aegilops ovata* and conducted crossing experiments in which he showed that *A. triticoides* was the result of pollinating *A. ovata* with wheat pollen. *A. triticoides* back crossed with wheat produced a still more wheat-like plant called *Aegilops speltaeformis.* These plants were partially self fertile and in one case remained constant with increased fertility in succeeding years.

A number of other investigators have crossed *Aegilops* with wheat. In most cases the F_1 plants were completely sterile. A detailed summary of this work has been presented by Leighty, Sandow and Taylor. These investigators have also made numerous crosses of *Aegilops* with different wheat species and obtained a few F_1 plants which were partially self fertile. Back crosses of *Aegilops ovata* × *Triticum* F_1 with wheat pollen produced 73 seeds from 3,088 flowers pollinated or 2.4 percent. These *A. speltaeformis* types thus obtained were partially selffertile.

The cytological analysis of *Aegilops* × *Triticum* hybrids is of great value in explaining the relationships of these two genera. If the Vulgare wheats are the result of hybrids between *Aegilops* and the Emmer wheats, some of the *Aegilops* chromosomes should be compatible with some of the Vulgare chromosomes. In the Emmer × Vulgare hybrids cytological studies indicated that the 14 Emmer chromosomes are com-

Fig. 1—12
Chromosome behavior at the first reduction divison of microsporemother cells

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Figures 1—4 were drawn from permanent preparations. All other figures are from aceto-carmine mounts.

Aegilops ovata × *T. dicoccum* F_1

Fig. 1. The 28 unpaired chromosomes in a typical divison stage.
Fig. 2. Irregular distribution of the chromosomes to the poles.
Figs. 3 and 4. Microspores resulting from the irregular reduction divisions.

patible with, and similar to, the 14 Vulgare chromosomes with which they pair. Apparently 14 of the 21 Vulgare chromosomes are from the Emmer wheats. We might expect then that the extra 7 Vulgare chromosomes would be compatible with 7 of the *Aegilops* chromosomes if the Vulgare wheats have originated from *Aegilops* × Emmer crosses.

Both *Aegilops ovata* and *A. cylindrica* have 14 pairs of chromosomes. In a cross of *Aegilops cylindrica* × *Triticum* the writer *et al*

found that there were approximately 7 pairs of chromosomes and 21 singles at the reduction division in F_1 anthers. Presumably 7 of the *Aegilops* chromosomes pair with 7 of the Vulgare chromosomes leave 7 *Aegilops* and 14 Vulgare chromosomes as univalent. In a similar cross using *A. ovata* instead of *cylindrica* Percival suggests that pairing occurs among the 14 *Aegilops* chromosomes, leaving the 21 Vulgare

Fig. 5

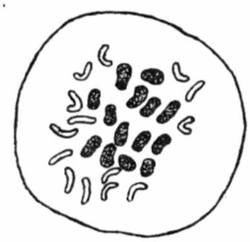

Fig. 6

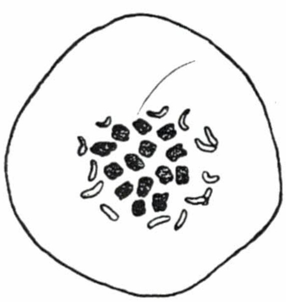

Fig. 7

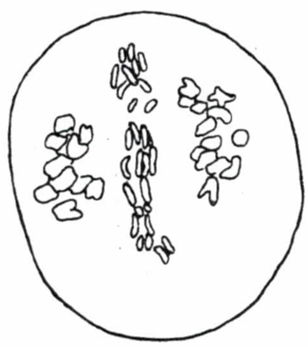

Fig. 8

(*Aegilops ovata* × *T. dicoccum*) F_1 × *T. dicoccum*

Figs. 5 and 6. Metaphase of first reduction division showing typical arrangement of 14 bivalents and 14 univalents.

Fig. 7. The 14 bivalents have divided and one group is shown as the split chromosomes approach the pole. The 14 univalents are still near the plate while the other 14 members of the bivalents are not included in this figure.

Fig. 8. A side view of a somewhat later stage than that shown in figure 7.

chromosomes as univalents in the F_1 reduction division. It is improbable, however, that the univalent chromosomes pair with each other since in a haploid plant of *T. vulgare* Gaines and Aase find no pairing of chromosomes at reduction and in wheat-rye hybrids Thompson finds no pairing of chromosomes at the first reduction division in F_1 plants.

In a cross of *Aegilops ovata* with an Emmer wheat Gaines and Aase find no pairing of chromosomes. The writer has found the same behavior in a cross of *A. ovata* × *T. dicoccum*. The random distribution of the unpaired chromosomes is shown in figures 1 and 2. The univalents apparently pass to one pole or the other at random without dividing. For the second reduction division the chromosomes divide

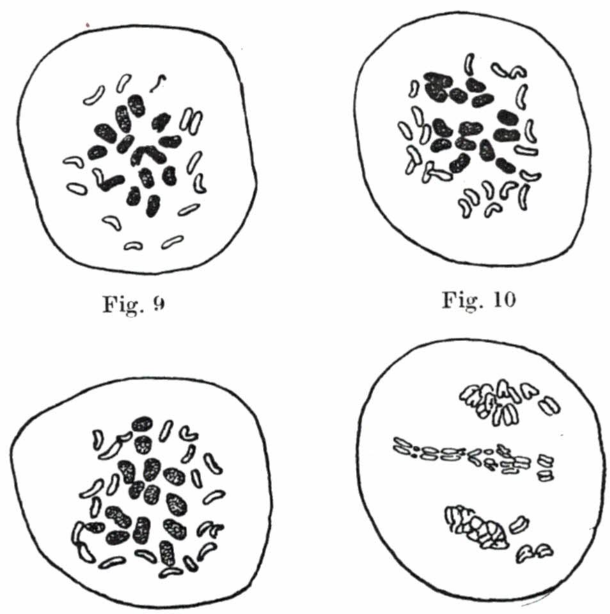

Fig. 9 Fig. 10

Fig. 11 Fig. 12

Aegilops ovata × *T. dicoccum* F_2 segregates.

Fig. 9. Metaphase showing 14 bivalent and 14 univalents.
Figs. 10 and 11. Metaphase showing 14 bivalents and 21 univalents.
Fig. 12. Typical behavior of 14 bivalents and 14 univalents in the first reduction division.

very irregularly and form microspores of various sizes and presumably with widely different chromosome numbers. The chromosomes are frequently not included in the nuclei and lie free in the cytoplasm or form small supernumerary nuclei in the microspores. Most of the tetrads are similar to the one shown in figure 4 but types such as shown in figure 3 are numerous. If chromosome assortment is at random the male gametes should have from 0 to 28 chromosomes. Sterility occurs in F_1 and dehiscence of anthers occurs only rarely. A total of 204 seeds were obtained

Figure 13

Above: *Aegilops ovata* and *Triticum dicoccum*.

Below: F_2 segregate of *A. ovata* × *T. dicoccum* and segregate of F_1 pollinated with *T. dicoccum*. These F_2 and back-cross segregates resemble *T. vulgare* in many respects. The plants are almost completely sterile and when mature the glumes are more compact and do not resemble the common wheats so closely.

from 1394 F_1 spikelets, — a surprising degree of fertility in view of the sterility of the anthers.

The F_2 segregates were very vigorous and were like the F_1 back crossed with Emmer to be described later. About 35 of these plants were grown in the greenhouse for cytological studies. A cytological study of $F_1 \times$ Emmer indicates that all functional F_1 egg cells have 28 chromosomes, so that F_2 chromosome counts can be analyzed on this basis.

Four F_2 plants had 14 pairs of chromosomes and 14 univalents at reduction of pollen mother cells as shown in figure 9. The bivalents divide normally but the singles lag an divide after the bivalents reach the poles (Fig. 12). In 8 plants there were 14 bivalents and 21 univalents at reduction as shown in figures 10 and 11. If the F_1 egg cells have 28 chromosomes then the functional male gametes have 14 and 21 chromosomes in the F_2 segregates described above. It is possible that the F_1 egg cells were pollinated with pollen from Emmer and Vulgare plants growing in the same field, although all of the F_1 heads which first appeared were used in back crosses and the heads which were open pollinated did not flower until most of the Emmer and Vulgare varieties has ceased shedding pollen. With random chromosome assortment the F_1 male gametes should have from 0 to 28 chromosomes and presumably those with chromosome numbers in multiples of 7 would be most functional. The high degree of fertility of F_1 egg cells suggest that the 28 chromosomes of the female gametes are not the result of random assortment of the chromosomes but are the result of non-reduction of the chromosomes. If non-reduction occurred in F_2 plants we might expect female gametes with 49 chromosomes and if chromosome behavior in pollen formation is typical of other wheat crosses the male gametes would have from 14 to 35 chromosomes in certain of the F_2 segregates. In F_3 it might be possible with such chromosome behavior to obtain, in rare cases, segregates with 84 chromosomes — twice the number found in the Vulgare wheats. In F_2 we already have segregates with 49 chromosomes. Unfortunately these F_2 plants are almost completely sterile; only 2 seeds were obtained from 180 F_2 heads. As shown in figure 14 these segregates are larger than typical plants of *T. vulgare* grown under the same conditions.

The cytological evidence so far supports the theory that the Vulgare wheats have originated from crosses of Emmer wheats and *Aegilops* species. *Aegilops cylindrica* has 7 chromosomes which pair with 7 Vulgare

chromosomes. Unfortunately no crosses of *A. cylindrica* with an Emmer wheat have been studied cytologically. *Aegilops ovata* chromosomes do

Figure 14

A typical F_2 segregate of *Aegilops ovata* × *Triticum dicoccum*. The back cross segregates, F_1 × *T. dicoccum* are essentially the same but have longer awns. A typical Vulgare variety, Marguis, is shown at the right

not pair with any the 14 Emmer chromosomes in the crosses studied by Gaines and Aase and the writer. These results support the suggestion made by Gaines and Aase that there are four sets of chro-

mosomes in these two genera. The Einkorn group has set A or B, the Emmer group sets A and B, the Vulgare group sets A, B and C, while *Aegilops cylindrica* or *A. ovata* has sets C and D. Presumably chromosome sets A and B of the Vulgare wheats came from the Emmer ancestors while set C was contributed by one of the *Aegilops* species.

These conclusions are further supported by cytological and genetic results with back crosses of *Aegilops ovata* × *T. dicoccum* F_1 pollinated with *T. dicoccum*. This cross was made to determine the chromosome number in the F_1 egg cells. From 714 F_1 flowers pollinated with *T. dicoccum* pollen 27 grains were obtained. Twelve plants were grown in the greenhouse and with one exception all plants appeared to be identical in morphological characters. A cytological study of 6 of these plants showed in every case 14 pairs of chromosomes and 14 univalents at the first reduction division. This result means that in every case studied the egg cell had 28 chromosomes, 14 from the Emmer parent and 14 from the *Aegilops* parent, due presumably to the absence of a normal reduction division. When such egg cells were pollinated with Emmer pollen the Emmer chromosomes presumably paired with the Emmer chromosomes of the F_1 plant leaving 14 *Aegilops* univalents in the reduction divison of the back crossed plants. This chromosome behavior at the first reduction division of the pollen mother cells is shown in figures 5, 6, 7 and 8. The bivalents divide normally. The univalents lag behind but ultimately divide. The second division is irregular and few normal pollen grains are found. Only 10 seeds were obtained from 65 heads.

These plants resulting from F_1 × Emmer have 28 Emmer chromosomes and 14 *Aegilops* chromosomes — the supposed chromosome combinations of *T. vulgare*, with the exception that the *Aegilops* chromosomes are not members of the same set of 7. Accordingly the irregular distribution of the *Aegilops* univalents results in a high degree of sterility. This chromosome combination does, however, result in plants which possess many of the typical Vulgare characters. When young, the plants have a rather spreading habit of growth resembling that of *Aegilops ovata* and the so-called "winter" wheats of the Vulgare group. There are usually about 10 culms per plant, even more than found in the Vulgare wheats when grown under the same conditions Fig. 14). The culms are hollow and thin walled; the rachis is non-fragile but disarticulates at the first node; the outer glumes are only slightly keeled, are broad at apex and are awned, often possessing a small secondary awn; the flowering glume is awned with a small secondary

awn in many cases; the leaf hairs are similar to those of the Vulgare wheats but are longer. The grain shape resembles that of the Emmer parent but in many other respects these segregates resemble the Vulgare wheats and particularly in those characters which distinguish the Emmer and Vulgare groups. These *Aegilops* × Emmer back crossed segregates might be even more like the Vulgare wheats and would be fertile and homozygous if the *Aegilops* chromosomes present consisted of a single diploid set instead of two sets in the haploid condition. In view of the antiquity of the Vulgare wheats it is also possible that many genetic changes have occurred since the origin of this group of wheat species.

The cytological work with wheat species and allied genera has shown the primary reason for sterility in wheat species hybrids, the cause of the unusual genetic results in partially sterile wheat hybrids and the difficulty in combining the desirable and typical characters of the Vulgare and Emmer wheats, and finally cytological studies have shown the probable origin of the bread wheats and suggest methods of producing new species which may be of even greater value.

Literature Cited

Gaines, E. F. and H. C. Aase. A haploid wheat plant. Amer. Jour. Bot. 13: 373—385. 1926.

Kihara, Hitoshi. Über cytologische Studien bei einigen Getreidearten. Bot. Mag. Tokio 32: 17—38, 21 text-figs. 1919.

— Über cytologische Studien bei einigen Getreidearten. III. Über die Schwankungen der Chromosomenzahl bei den Speciesbatsarden der *Triticum*-Arten. Bot. Mag. Tokio 35: 19—44. 1921.

Leighty, C. E., W. J. Sandow, and J. W. Taylor. Intergeneric hybrids in *Aegilops*, *Triticum*, and *Secale*. Jour. Agr. Research 33: 101—141, fig. 18. 1926.

Malinowski, Edmund. Linkage phenomena in wheat. Jour. Genetics 17: 157—185. 1926.

Mol, W. de. De Reductiedeeling bijeenige *Triticum*-soorten. Genetica 6: 289—324. 1924.

Nicolaeva, M. A. Cytological investigations of the genus *Triticum*. Bull. applied Bot. 13: 33—44. 1923.

Percival, J. The wheat plant. 463 p. illus. London: 1. Duckworth & Co. 1921.

— The morphology and cytology of some hybrids of *Aegilops ovata* L.♀ × wheats♂. Jour. Genetics 17: 49—68, pls. 6. 1926.

Sakamura, Tetsu. Kurze Mitteilung über die Chromosomenzahlen und die Verwandtschaftsverhältnisse der *Triticum*-Arten. Bot. Mag. of Tokyo 32: 150—153. 1918.

Sax, Karl. Sterility in wheat hybrids, II. Chromosome behavior in partially sterile hybrids. Genetics 7: 513—552. 1922.

— The relation between chromosome number, morphological characters and rust resistance in segregates of partially sterile wheat hybrids. Genetics 8: 301—321. 1923.

Sax, Karl and E. F. Gaines. A Genetic and cytological study of certain hybrids of wheat species. Jour. Agr. Research 28: 1017—1032, pls. 2. 1924.

Sax, K. and H. J. Sax. Chromosome behavior in a genus cross. Genetics 1: 454—464. 1924.

Stolze, K. V. Die Chromosomenzahlen der hauptsächlichsten Getreidearten neben allgemeinen Betrachtungen über Chromosomen, Chromosomenzahl und Chromosomengröße im Pflanzenreich. Biblioth. Genetica 8: 1—71. 1925.

Thompson, W. P. Chromosome behavior in triploid wheat hybrids. Jour. Genetics 17: 43—48, fig. 8. 1926.

— Chromosome behavior in a cross between wheat and rye. Genetics 11: 317—332, fig. 9. 1926.

— The correlation of characters in hybrids of *Triticum durum* and *Triticum vulgare*. Genetics 10: 285—304. 1925.

Tschermak, Erich und Hubert Bleier. Über fruchtbare *Aegilops*-Weizenbastarde. Beispiele für die Entstehung neuer Arten durch Bastardierung. Ber. d. Deutsch. Bot. Ges. 44: 110—132. 1926.