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Weizen (*Triticum* L.)

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I. The Systematics, Cytology and Genetics of Wheat

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A. Origin and relationships

1. Classification

Like many other cultivated plants, the wheats are difficult material taxonomically. Many of the differences between types have been broken down by the activities of breeders, and there is a strong temptation to give undue consideration to minor differences which happen to be of agronomic importance. However, the wheats fall naturally into three groups, which have long been recognized, the diploids (n = 7), the tetraploids (n = 14), and the hexaploids (n = 21). It is in disposing of the various entities within these groups that disagreement has arisen.

In the first edition of the Handbuch, von Rosenstiel (1950) followed Schiemann's (1948) treatment. No important changes have since been proposed for the diploid and tetraploid groups, except one (*Triticum turanicum*) made by Schiemann (1951) herself. For the hexaploids, however, Mac Key (1954b) has suggested a classification which has much to recommend it. His treatment is followed here (table 34).

Table 34. The species of *Triticum*

		Diploid group n = 7	Tetraploid group n = 14	Hexaploid group n = 21
Wild forms		*T. boeoticum* Boiss. em. Schiem. (= *aegilopoides* Bal.)	*T. dicoccoides* Körn. *T. timopheevi* Zhukov	
Cultivated forms	Spelt types	*T. monococcum* L.	*T. dicoccum* Schübl.	*T. aestivum* L. em. Thell. ssp. *spelta* (L.) Thell. *T. aestivum* ssp. *macha* (Dek. *et* Men.) Mac Key *T. aestivum* ssp. *vavilovi* (Tuman.) Sears, n. comb.
	Naked types		*T. durum* Desf. *T. turgidum* L. *T. turanicum* Jakubz. (= *orientale* Perc.) *T. polonicum* L. *T. carthlicum* Nevski (= *persicum* Vav.)	*T. aestivum* ssp. *vulgare* (Vill., Host) Mac Key *T. aestivum* ssp. *compactum* (Host) Mac Key *T. aestivum* ssp. *sphaerococcum* (Perc.) Mac Key

The essential difference between the hexaploid grouping recommended by MAC KEY and that by SCHIEMANN is that MAC KEY considers all the five types to be subspecies of *T. aestivum*, whereas SCHIEMANN lists only one, *compactum*, as a subspecies. MAC KEY argues that it is unrealistic to recognize different species of hexaploid wheat, saying that "there are no real species barriers within the hexaploid wheat." The various types can easily be crossed, and chromosome pairing is often as good in inter-group hybrids as in hybrids between varieties belonging to the same group. So far as *compactum*, *spelta*, and *sphaerococcum* are concerned, each of these types differs from *vulgare* by only one gene. To single out *compactum* as a subspecies, while giving the other three types specific rank, as SCHIEMANN does, can possibly be justified by the fact that *vulgare* and *compactum* are widely grown, often together in the same region, and have been extensively intercrossed by plant breeders; while *spelta* and *sphaerococcum* are restricted in distribution and have seldom been used as breeding material in the important wheat-growing regions of the world. However, it seems inevitable that *spelta* and *sphaerococcum* will become less and less isolated as the practice of plant breeding spreads into the regions where they are grown. For the sake of consistency, then, and to have a system of classification which provides for future developments, MAC KEY's treatment appears to warrant acceptance. Furthermore, there is an advantage to having a *vulgare* group. This name, long applied to common wheat, has now been ruled inacceptable at the specific level. The establishment of a *vulgare* subspecies would preserve the most familiar and widely used designation for common wheat.

Although relatively little is known of the genetics of the characters distinguishing *T. aestivum* ssp. *macha* and ssp. *vavilovi*, it has been shown (SACHS, 1953a), that both cross readily with the other hexaploid wheats and give chromosome pairing comparable to that in other sub-specific crosses in this group. One variety of ssp. *macha* produces semi-lethal hybrids in crosses with other hexaploids, but at least one variety does not. The differences between *macha* and *spelta*, *vulgare*, and *compactum* are believed by SACHS to depend upon a number of genes, but MAC KEY (1954b) feels that the really fundamental differences may be fairly simply inherited. At any rate, in the absence of effective barriers to crossing, specific rank for *macha* does not appear to be justified. Neither does *vavilovi* seem to deserve specific rank. Data are not available concerning the inheritance of *vavilovi*'s distinguishing characteristics, but it seems unlikely that a type which crosses so readily with *vulgare* and the other hexaploids can differ in a very complex way. It is such a distinctive type, however, that it can scarcely be omitted or relegated to inferior status.

There is some question whether types differing by single genes should be given even subspecific rank. MAC KEY points out, however, that "the groups are morphologically distinct and the decisive characteristics are so profound as to be of definite agronomic significance." Possibly if the hexaploid wheats were of no practical value, and if it were known that the differences between the types were due to single genes, something less than subspecific rank would be given to *vulgare*, *spelta*, *compactum*, and *sphaerococcum*. In classifying cultivated plants, however, it is difficult not to attach importance to such differences as exist here.

Both VON ROSENSTIEL (1950) and MAC KEY (1954b) question the value of varietal classifications such as those of KÖRNICKE (1885) and MANSFELD (1951) based on morphological characters, at least on a world-wide scale. Not only are designations likely to be cumbersome, but biotypes are included in the same artificial variety which, while superficially alike, may differ greatly physiologically and in ecological requirements. MAC KEY feels that the agronomic varieties are the only satisfactory subdivision. The varieties can then be grouped by the countries of their origin, and this tends

to keep together those with similar adaptation. Within the various countries, keys based on morphological characters can be made if desired.

There is, of course, an obvious inconsistency in the classification given in table 34, in that the different hexaploid wheats are considered subspecies while the tetraploid wheats, some of which also differ from each other by single genes, are regarded as full species. Indeed, *T. carthlicum* differs from *T. dicoccum* by the same gene, Q, as distinguishes ssp. *vulgare* from ssp. *spelta*. Both *T. turgidum* and *T. polonicum* differ from *T. durum* primarily in single genes. Since less breeding work has been done with the tetraploids, however, the different groups have tended to remain more distinct. Consequently, the groups probably more nearly comprise phylogenetic units and are more homogeneous as to physiological and ecological characteristics. The different "species" cross freely, however, and eventually it will probably be desirable to combine them into a single species.

T. timopheevi has generally been regarded as having one set of seven chromosomes different from either set of seven of the other tetraploid wheats. SACHS (1953b) shows, however, that the chromosome differences are probably insignificant, in as much as a variety of *T. dicoccoides* has been found which gives much better chromosome pairing in hybrids with *T. timopheevi* than it does in hybrids with another variety of *T. dicoccoides*. LOVE (1941) had earlier suggested that the chromosomes of *T. timopheevi* were not much more different from those of the common tetraploids than were those of certain other aberrant types, such as Pentad durum.

SACHS' results with *T. dicoccoides* × *T. timopheevi* tend to confirm SCHIEMANN's (1948) refusal to recognize *T. armeniacum* (STOL.) NEVSKI as a separate species. She considers it merely a variety of *T. dicoccum*. An important reason why *armeniacum* had been given specific rank was the similarity of its chromosomes to those of *T. timopheevi*. Now that the aberrant chromosome pattern has been shown not necessarily to be of any taxonomic significance, there seems little reason to split off *armeniacum*.

2. Origin

The wheats have long been known to constitute an allopolyploid series. The three groups have 7, 14, and 21 pairs of chromosomes, respectively, and hybrids between hexaploids and tetraploids and between tetraploids and diploids have shown that only three different sets of seven chromosomes are involved in all three groups. These sets are designated the A, B, and D "genomes", the diploid species being AA, the tetraploids AABB, and the hexaploids AABBDD.

It was realized by 1928 that the D genome must have been contributed by a species of *Aegilops*, for SAX and SAX (1924) had already shown that hybrids of *Ae. cylindrica* (n = 14) with hexaploid wheat usually had seven pairs of chromosomes, and BLEIER in 1928 found that hybrids of *cylindrica* with tetraploids had mostly no pairs. It was not until 1944, however, that the DD species was actually identified. In that year MCFADDEN and SEARS reported the synthesis of a *T. dicoccoides* × *Ae. squarrosa* amphiploid which closely resembled *T. aestivum* ssp. *spelta* and showed good chromosome pairing in hybrids with *spelta* and *vulgare*. At the same time KIHARA (1944) was independently suggesting *Ae. squarrosa* as the contributor of the D genome. It seems clear that the D genome came from *Ae. squarrosa* and that the hexaploid group arose in relatively recent times, subsequent to the cultivation of wheat by man.

Concerning the origin of the tetraploid (emmer) group, one view frequently expressed is that the group arose through autotetraploidy. VON ROSENSTIEL (1950) points out that this must have occurred long ago, for the B genome has subsequently become

so strongly differentiated that it is today no longer homologous with the A genome. Actually, relegating the autotetraploid origin of the emmer group to the distant past does not solve the problem of the differentiation of the B genome. An autotetraploid of an einkorn would have been AAAA, and it is extremely improbable that seven pairs of its chromosomes could ever have differentiated into the B genome while the other seven pairs remained relatively unchanged. No mechanism for changing the homology of chromosomes is known which could very well have singled out seven of the fourteen chromosomes and left the other seven virtually unaffected.

It is a reasonable assumption that the emmer group arose as an allotetraploid involving *T. boeoticum* (einkorn) and a diploid species of either *Agropyron* or *Aegilops*. McFADDEN and SEARS (1946) pointed out that *Agropyron triticeum* GAERTNER (n = 7) could have contributed the characters of the tetraploid wheats which are lacking among the einkorns (notably the free-threshing characteristic), and suggested *triticeum* as a possible source of the B genome. AVDULOV (1931), however, had already shown that the chromosomes of *A. triticeum* (= *A. prostratum* [PALL] P. BEAUV.) have sub-terminal centromeres; and this is a type of chromosome not represented in wheat.

It is of course possible that the B genome has passed out of existence, except as preserved in the wheats. It is also possible that some species of *Aegilops*, perhaps *Ae. bicornis*, supplied the bulk of the B genome, with only one or a few chromosome segments having been derived from some such species as *A. triticeum*. An *Ae. bicornis* × *T. monococcum* amphidiploid produced by the writer (unpublished) exhibited chromosome pairing in hybrids with *T. dicoccum* such that the calculated $B_{bicornis}$ B_{emmer} contribution was not conspicuously less than that attributable to $A_{einkorn}$ A_{emmer} association. The *bicornis-monococcum* amphidiploid was very similar to *T. dicoccum* in morphological characters, according to E. S. McFADDEN (private communication). McFADDEN suggested that *Ae. bicornis* (or *Ae. speltoides*) must have supplied the B genome of *T. dicoccum*.

Within the hexaploid group, in particular, there has been much speculation as to the relative antiquity of the various subspecies. Ssp. *spelta* was considered the most primitive hexaploid wheat until SCHIEMANN in 1931 pointed out that it was grown in only a limited area in southwestern Europe, far from the region of presumed origin of the hexaploid wheat, southeastern Europe or the Near East. McFADDEN and SEARS (1946) revived the theory of the primitiveness of *spelta*, suggesting that it had originated in the Caucasus region and had been transported via a northern route to western Europe. There it had hybridized with *T. carthlicum*'s tetraploid progenitor (the free-threshing, small-kerneled, compact-spiked Lake Dweller Wheat, *T. antiquorum* HEER., previously considered to be hexaploid rather than tetraploid) and had given rise to *vulgare*. The agronomically more desirable free-threshing *vulgare* then replaced *spelta* throughout all of its range except the small areas in southwestern Europe.

SCHIEMANN (1951) and BERTSCH (1950) disagree with the essential points of the McFADDEN-SEARS argument. They maintain that if *spelta* really preceded *vulgare*, some archaeological evidence ought to exist for its antiquity, and it should not be confined today to such a limited area as it is. Also, they insist that the Lake Dweller wheat was actually hexaploid, not tetraploid.

Assuming that the distributional areas of *T. dicoccum*, *T. dicoccoides*, and *T. carthlicum* all overlapped that of *Ae. squarrosa* in ancient times as they do now, three different modes of origin are possible for both *spelta* and *vulgare*. *Spelta* may have arisen (1) as an amphiploid of *dicoccum* (or *dicoccoides*) × *Ae. squarrosa*, (2) as a segregate from *vulgare* (or *compactum*) × *dicoccum*, or (3) as a mutant from *vulgare*. *Vulgare* may have arisen (1) as an amphiploid of *carthlicum* × *Ae. squarrosa*, (2) as a segregate from *spelta*

× *carthlicum*, or (3) as a mutant from *spelta*. Thus the exact method of origin of either *spelta* or *vulgare* may be very difficult to determine, even though archaeological evidence may eventually establish which arose first.

MAC KEY (1954a) believes that *compactum* is the oldest of the present-day subspecies of *T. aestivum*. He says that "the original hexaploid wheat undoubtedly had a more or less fragile rachis," and that the *compactum* gene C, when it appeared, made the rachis tough. Present-day *vulgare* he believes to have arisen following the accumulation of genes other than C for tough rachis. *Spelta* is believed to have arisen more then once, first through hybridization of *dicoccum* with *compactum*, and again, through loss of Q, the speltoid-suppressing gene, from *vulgare* (to give the so-called *speltiforme* types).

The fact that *T. antiquorum* had a compact spike and may only have been a variant of *compactum* favors MAC KEY's idea of the antiquity of *compactum*. Whether the hexaploid types that preceded *compactum* necessarily had fragile spikes, however, is open to some question. Although both A and D genomes contribute genes for brittleness, as MAC KEY points out, the brittleness affects different regions of the rachis, and AD amphidiploids have a reasonably tough rachis (SEARS, 1941a). KIHARA and LILIENFELD (1949) found *T. carthlicum* × *Ae. squarrosa* to have a fragile rachis, but on the other hand, even *T. dicoccum* × *Ae. squarrosa* is not highly fragile (SEARS, unpublished).

Whether or not the first hexaploids had fragile rachises, it seems clear that they were non-*compactum*. Since the *compactum* gene is in the D genome, a newly produced hexaploid of *compactum* type would necessarily have arisen from an *Ae. squarrosa* carrying this gene. Not only has no such *Ae. squarrosa* been reported, but it is difficult to imagine a viable *squarrosa* possessing a gene with such an extreme effect as C would almost certainly have in a diploid species. Even in the hexaploid the effect of C is profound. It is more reasonable to suppose that C arose as a mutant subsequent to the establishment of the hexaploid group rather than before.

A point similar to the foregoing can be made concerning ssp. *sphaerococcum*, which is differentiated by a single gene on chromosome XVI. It seems likely that the *sphaerococcum* gene also appeared following the origin of the hexaploid group rather than before. In this case the argument agrees with the evidence from other sources, ELLERTON (1939) having concluded from distributional data that *sphaerococcum* had been derived from *vulgare*. He also suggested that the *sphaerococcum* gene was a deficiency mutation; but subsequent work (SEARS, 1947) shows that the "normal" allele of *sphaerococcum*, rather than *sphaerococcum* itself, is the null allele. This might be taken to suggest that *vulgare*, rather than *sphaerococcum*, is deficient at the locus concerned, and that *vulgare* had arisen from *sphaerococcum* through simple deficiency. Although it is probable that *vulgare* can be obtained in this way, it seems more likely that the *vulgare* allele is not a deficiency but is a gene covered by duplicate genes at other loci, and that this gene gave rise to the *sphaerococcum* allele through a radical mutation (SEARS, 1954).

The same argument can be made concerning *spelta* and *vulgare*: that the *spelta* gene q is not a deficiency but is a gene behaving as a null allele because it is duplicated at other loci; and that *spelta* gave rise to *vulgare* through mutation of q to Q. In this case, however, the argument loses weight because Q is believed to be in the B genome (certainly not in the D genome), and hence did not have to occur in *Ae. squarrosa* in order for *vulgare* to be the more primitive. It may have occurred as a mutation in the tetraploid wheats, where both Q and q exist today, or it may have been introduced to the tetraploids from such a species as *Agropyron triticeum*, as MCFADDEN and SEARS (1946) have suggested.

Concerning the origin of the species within the tetraploid group, relatively little can be said. It is supposed that *T. dicoccum* stands closest to the wild species *T. dicoccoides*.

Each other species except *T. timopheevi* may then have been derived from *T. dicoccum* by one or a few gene mutations. *T. timopheevi*, one of whose genomes differs so greatly as to have been designated by a different letter (G instead of B) has been the greatest problem in the genus. It seems probable that *T. timopheevi* originated either as a different amphidiploid from the one which gave rise to the other tetraploid wheats, or as the result of a later cross of *T. dicoccoides* or *T. dicoccum* with a species from another genus. Evidently, subsequent crossing of *T. timopheevi* with *T. dicoccoides* and *T. dicoccum* has resulted in the transfer of the *timopheevi* chromosome pattern to at least one variety of each of these species. That this has occurred suggests that the genes which distinguish *T. timopheevi* from the other tetraploid wheats are not associated with the chromosomal differences. It further suggests that these genes are not large in number.

3. Hybrids and amphiploids

Species of the genus *Triticum* can be hybridized with species of all four other genera of the sub-tribe *Triticinae* — namely, *Secale*, *Aegilops*, *Agropyron*, and *Haynaldia*. These five genera all have a basic chromosome number of seven and are believed to have originated from a common ancestor. The D genome of the hexaploid wheats is equivalent to that of *Ae. squarrosa*, and genome B has often been assumed to have come from *Agropyron*. It is therefore of interest to consider some of the results of hybridization of *Triticum* with these related genera. The amphiploids which have been produced, being essentially new species, are of sufficient importance to merit listing (table 35). The intra-*Triticum* amphiploids which have been obtained are also listed in table 35.

Table 35. *Triticum* amphiploids

Combination	n	First produced by
T. durum × *T. monococcum*	14 + 7	Thompson, 1931
T. dicoccoides × *T. boeoticum*	14 + 7	Bell and Sachs, 1953
T. monococcum × *T. carthlicum*	7 + 14	Kasparyan, 1940
T. timopheevi × *T. monococcum*	14 + 7	Kostoff, 1936
T. durum × *T. timopheevi*	14 + 14	Zhebrak, 1939
T. carthlicum × *T. timopheevi*	14 + 14	Zhebrak, 1941a
T. turgidum × *T. timopheevi*	14 + 14	Zhebrak, 1941b
T. polonicum × *T. timopheevi*	14 + 14	Zhebrak, 1944a
T. dicoccum × *T. timopheevi*	14 + 14	Bell and Sachs, 1953
T. dicoccoides × *T. timopheevi*	14 + 14	Bell and Sachs, 1953
T. timopheevi × *T. turanicum*	14 + 14	Bell and Sachs, 1953
T. durum × *T. aestivum*	14 + 21	Zhebrak, 1944b
T. timopheevi × *T. aestivum*	14 + 21	Zhebrak, 1943
T. monococcum × *Ae. uniartstata*	7 + 7	Sears, 1939b
Ae. speltoides × *T. monococcum*	7 + 7	Sears, 1941
Ae. bicornis × *T. monococcum*	7 + 7	Sears, unpub.
T. aegilopoides × *Ae. squarrosa*	7 + 7	Sears, 1941a
T. aegilopoides × *Ae. umbellulata*	7 + 7	Sears, 1941a
T. aegilopoides × *Ae. uniaristata*	7 + 7	Sears, 1941a
T. aegilopoides × *H. villosa*	7 + 7	Sears, unpub.
Ae. caudata × *T. dicoccum*	7 + 14	Oehler, 1934
Ae. longissima × *T. durum*	7 + 14	Sorokina, 1937
Ae. longissima × *T. polonicum*	7 + 14	Sando, 1935
Ae. caudata × *T. turgidum*	7 + 14	Bell and Sachs, 1953
Ae. caudata × *T. durum*	7 + 14	Bell and Sachs, 1953
T. turgidum × *Ae. speltoides*	14 + 7	Britten and Thompson, 1941
T. dicoccoides × *Ae. speltoides*	14 + 7	McFadden and Sears, 1946

Continuation of table 35

Combination	n	First produced by
T. dicoccoides × *Ae. caudata*	14 + 7	McFADDEN and SEARS, 1946
T. dicoccoides × *Ae. squarrosa*	14 + 7	McFADDEN and SEARS, 1946
T. dicoccoides × *Ae. umbellulata*	14 + 7	McFADDEN and SEARS, 1946
T. dicoccoides × *Ae. comosa*	14 + 7	McFADDEN and SEARS, 1946
T. dicoccoides × *Ae. longissima*	14 + 7	McFADDEN and SEARS, 1946
T. carthlicum × *Ae. longissima*	14 + 7	McFADDEN and SEARS, 1946
T. dicoccum × *Ae. longissima*	14 + 7	McFADDEN and SEARS, 1946
T. dicoccoides × *Ae. uniaristata*	14 + 7	McFADDEN and SEARS, 1946
T. timopheevi × *Ae. umbellulata*	14 + 7	McFADDEN and SEARS, 1947
T. timopheevi × *Ae. caudata*	14 + 7	McFADDEN and SEARS, 1947
T. timopheevi × *Ae. speltoides*	14 + 7	McFADDEN and SEARS, 1947
T. timopheevi × *Ae. bicornis*	14 + 7	McFADDEN and SEARS, 1947
T. timopheevi × *Ae. uniaristata*	14 + 7	McFADDEN and SEARS, 1947
T. timopheevi × *Ae. squarrosa*	14 + 7	McFADDEN and SEARS, 1947
Ae. ovata × *T. boeoticum*	14 + 7	BELL and SACHS, 1953
Ae. cylindrica × *T. boeoticum*	14 + 7	BELL and SACHS, 1953
Ae. ovata × *T. dicoccoides*	14 + 14	TSCHERMAK and BLEIER, 1926
Ae. ovata × *T. durum*	14 + 14	TSCHERMAK and BLEIER, 1926
Ae. ovata × *T. turgidum*	14 + 14	TSCHERMAK, 1929
Ae. ovata × *T. dicoccum*	14 + 14	TSCHERMAK, 1929
Ae. ovata × *T. timopheevi*	14 + 14	BELL and SACHS, 1953
Ae. triuncialis × *T. dicoccum*	14 + 14	OEHLER, 1934
Ae. triuncialis × *T. durum*	14 + 14	OEHLER, 1936
Ae. triuncialis × *T. dicoccoides*	14 + 14	SOROKINA, 1937
Ae. triuncialis × *T. polonicum*	14 + 14	SOROKINA, 1937
Ae. cylindrica × *T. durum*	14 + 14	SEARS, 1944b
Ae. cylindrica × *T. carthlicum*	14 + 14	BELL and SACHS, 1953
Ae. ventricosa × *T. dicoccum*	14 + 14	SOROKINA, 1938
Ae. ventricosa × *T. turgidum*	14 + 14	BLARINGHEM, 1936
Ae. ventricosa × *T. dicoccoides*	14 + 14	SIMONET, 1953
Ae. cylindrica × *T. aestivum*	14 + 21	KIHARA and KATAYAMA, 1931
T. durum × *A. intermedium*	14 + 21	KIHZNYAK, 1937
T. dicoccum × *A. intermedium*	14 + 21	KIHZNYAK, 1937
T. turgidum × *A. intermedium*	14 + 21	KHIZNYAK, 1937
T. polonicum × *A. intermedium*	14 + 21	KIHZNYAK, 1937
T. carthlicum × *A. intermedium*	14 + 21	KIHZNYAK, 1937
T. aestivum × *A. intermedium*	21 + 21	PETO, 1938
T. durum × *S. cereale*	14 + 7	O'MARA, 1948
T. durum × *S. montanum*	14 + 7	DERZHAVIN, 1938
T. turgidum × *S. cereale*	14 + 7	NAKAJIMA, 1952
T. aestivum × *S. cereale*	21 + 7	RIMPAU, 1891
T. aegilopoides × *H. villosa*	7 + 7	SEARS, unpub.
T. turgidum × *H. villosa*	14 + 7	TSCHERMAK, 1930
T. dicoccum × *H. villosa*	14 + 7	KOSTOFF and ARUTIUNOVA, 1937
T. dicoccoides × *H. villosa*	14 + 7	McFADDEN and SEARS, 1947

a. Triticum-Aegilops

The chief interest in this combination has resided in the part played by *Aegilops* in the origin of wheat — particularly of the hexaploid group. A noteworthy achievement has been made, particularly by KIHARA and his associates, in the determination of the relationships among the 19 species of *Aegilops*. Table 36 gives the genomic formulae determined for 18 of the species by KIHARA (LILIENFELD, 1951). It will be noted that the nine diploid species have genomes which are to some degree differentiated from each other structurally. The polyploid species, nearly all tetraploid, are amphidiploids formed in every case but one from hybrids of species identical with, or similar to

existing diploids in chromosome content. The one species not included in KIHARA's analysis is *Ae. juvenalis* (THELL.) EIG (n = 21; = *Ae. turcomanica* ROSH.) of the *Vertebrata* group. Certain types formerly regarded as species are included by KIHARA in other species; namely, *Ae. kotschyi* BOISS. in *Ae. variabilis*, *Ae. persica* BOISS. in *Ae. triuncialis*, *Ae. heldreichii* HOLZM. in *Ae. comosa*, *Ae. aucheri* BOISS. in *Ae. speltoides*, and *Ae. sharonensis* EIG in *Ae. longissima*.

Recently some of the *Aegilops* species have attracted attention because of their resistance to certain diseases (JOHNSTON, 1940) and insects (JONES, 1939), and because of the possibility of transferring *Aegilops* resistance to common wheat. SEARS (1955) reports the transfer of leaf-rust resistance from *Ae. umbellulata* to *T. aestivum* ssp. *vulgare*. The procedure involved the use of a bridging species, *T. dicoccoides*, to combine the *vulgare* and *umbellulata* chromosomes; the production of an alien addition race, having a single pair of *umbellulata* chromosomes added to wheat; and the X-irradiation of addition monosomics to translocate a resistance-carrying segment of the *umbellulata* chromosome to a wheat chromosome.

Table 36. Classification of the species of the genus *Aegilops* according to KIHARA

Species	Formula
Polyeides:	
Ae. umbellulata ZHUK.	C^u
Ae. ovata L.	C^uM^o
Ae. triaristata WILLD. 4×	C^uM^t
Ae. triaristata WILLD. 6×	$C^uM^t+(?)$
Ae. columnaris ZHUK.	C^uM^c
Ae. biuncialis VIS.	C^uM^b
Ae. variabilis EIG	C^uS^v
Ae. triuncialis L.	C^uC
Cylindropyrum:	
Ae. cylindrica HOST	CD
Ae. caudata L.	C
Comopyrum:	
Ae. comosa SIBTH. et SM.	M
Ae. uniaristata VIS.	M^u
Amblyopyrum:	
Ae. mutica BOISS.	Mt
Sitopsis:	
Ae. speltoides TAUSCH	S
Ae. longissima SCHW. et MUSCH.	S^l
Ae. bicornis (FORSK.) JAUB. et SPACH	S^b
Vertebrata:	
Ae. squarrosa L.	D
Ae. crassa BOISS. 4×	DJ
Ae. crassa BOISS. 6×	DJ+(?)
Ae. ventricosa TAUSCH	DM^v

Considerable practical interest attaches to the discovery that *Ae. squarrosa* possesses the D genome of hexaploid wheats. In the first place, any desirable genes in this species can be transferred to common wheat with relative ease, simply by making a synthetic ABD amphiploid involving *squarrosa* and using this material as the source of the desired genes. No characters of value, such as disease resistance, have been reported in *Ae. squarrosa*, but a more comprehensive collection of *squarrosa* varieties might reveal something of worth.

A second use of *Ae. squarrosa* involves adding it to various tetraploid wheats through amphiploidy. This converts these wheats to hexaploids which can then be crossed to common wheats without the sterility and inviability normally encountered in F_1, F_2, and later generations of emmer-*vulgare* hybrids. Such artificial hexaploids have already been made (SEARS, unpublished) involving the *durum* varieties Iumillo, Carleton, Pentad, Golden Ball, and PI 94587, and the emmer variety Vernal. KIHARA et al. (1950) report additional artificial hexaploids involving *Ae. squarrosa* and *T. durum*, *T. turgidum*, and *T. carthlicum*.

b. Triticum-Agropyron

The principal interest in hybridization of *Triticum* with *Agropyron* has been in the possibility of transferring desirable characters to wheat. Such *Agropyron* characters as winter hardiness, drought resistance, disease resistance, alkali resistance, and possibly perennial habit would be of great value if they existed in wheat.

The earlier hybridization work was thoroughly reviewed by VON ROSENSTIEL (1950) in the first edition of the Handbuch. Only two species of *Agropyron* have been extensively crossed with *Triticum*, *A. elongatum* (HOST) BEAUV. (n = 35) and *A. intermedium* (HOST) PAL. (n = 21; = *A. glaucum*). *A. trichophorum* (LINK) RICHT., which has been used by a number of breeders in the U.S.A., is believed (GAUL, 1953) to belong in *A. intermedium*, as ssp. *trichophorum* (LINK) VOLKHART. The chromosome numbers given for *A. elongatum* and *A. intermedium* are those of the types chiefly used in crosses. *A. elongatum* also has forms with 7, 21, and 28 pairs, and *A. intermedium* has a 14-pair variant.

Recent works of GAUL (1953) and STEBBINS and PUN (1953) have given a somewhat different picture of the relationships of *A. intermedium* and *A. elongatum* with *Triticum* than was formerly accepted. Most credence had been given to the proposal of PETO (1936) that *A. intermedium* had the genomic formula AXY and that *A. elongatum* was A (or B) XXYY. MATSUMURA (1951) presented evidence that the emmer genome involved was B rather than A and suggested the use of E and F instead of X and Y; *A. intermedium* thus became BEF and *A. elongatum* BEEFF.

In their studies of *Secale cereale* × *A. intermedium*, STEBBINS and PUN (1953) found that practically the only pairing which occurred was autosyndesis of *Agropyron* chromosomes, and that the amount of pairing was essentially the same as that observed by other investigators in hybrids of wheat with *A. intermedium*. Therefore, they concluded that *A. intermedium* has no genome in common with the wheats, and gave it the formula E_1E_2N (or $E_1N_1N_2$). *A. elongatum* they believed to have one genome related to wheat and at least one related to *A. intermedium*. The formula they suggested for *A. elongatum* was $B_2E_1E_2F_1F_2$.

GAUL (1953) has carried the analysis of *A. intermedium* a step further, by study of meiosis in relatively large numbers of plants from three different crosses, all three of which involved the same *A. intermedium* parent individuals. He analyzed 9 hybrid plants of *Secale cereale* × *A. intermedium*, 28 of *T. durum* and *T. dicoccum* × *A. intermedium*, and 40 of *T. aestivum* ssp. *vulgare* × *A. intermedium*. Great variation in pairing was encountered, particularly in *vulgare* × *intermedium*, where averages of 1.34 to 13.86 "Bindungen" (bivalents + trivalents + quadrivalents × 2) per microsporocyte were observed for the various plants. This variation in pairing was shown to be due largely to genetic differences between the hybrid individuals — differences which led to the imposition of varying degrees of desynapsis upon the fundamental pairing pattern. (Desynapsis was also noted by THOMPSON and GRAFIUS 1950, in hybrids of var. *trichophorum* × *vulgare*). By considering the relationship between the number of chiasmata per paired chromosome and the percentage of chromosomes paired of those potentially able to pair, GAUL (1954) has developed a formula which permits calculation of the number of potentially pairing chromosomes from the data for each individual plant, whether the plant is low or high in amount of pairing (More accurate results came from the plants with nearest to the maximum amount of pairing.) The formula is: $p = \frac{X^2 + X - B}{(2X - B) \cdot Z}$ in which p is the number of chromosomes per cell able to pair, X is the total number of chiasmata counted in the cells studied in the particular pre-

paration, B is the total number of chromosomes involved in pairing, and Z is the total number of cells.

The maximum number of paired chromosomes observed was 37, 26, and 22, respectively, in the hybrids involving *vulgare*, *durum* (or *dicoccum*), and *S. cereale*; but GAUL (1953) shows by use of his formula that about 40, 32, and 20 chromosomes actually had pairing affinity. From these figures he proceeds to the conclusion that *A. intermedium* is of the genomic constitution $I_1I_2X_m$. This is essentially the conclusion reached independently by STEBBINS and PUN, except for the use of different letters; and GAUL agrees with them that all pairing in the *Secale* × *A. intermedium* hybrid is autosyndetic. However, he believes that X_m, rather than being unrelated to any of the genomes of *Triticum*, has weak affinity to AB and pairs strongly with the D genome. Thereby he accounts for the increased pairing in *durum* × *intermedium* over *Secale* × *intermedium*, and also for the further increase in *vulgare* × *intermedium*. In the latter hybrid he believes that the X_m chromosomes pair fairly regularly with those of the D genome and occasionally pair also with those of A or B to give multivalent configurations.

GAUL suggests that the genome X_m comes from *Aegilops mutica*. The chromosomes of this species have the required strong affinity with the D genome (*Ae. squarrosa*) and weak affinity with AB. Furthermore, *Ae. mutica* has morphological similarities to *A. intermedium*.

Until additional work has been done with *A. elongatum* and its hybrids, its genomic constitution must remain in some doubt. It is generally believed to have at least one genome in common with *A. intermedium*. If this is X_m, *elongatum* should show more chromosome pairing in hybrids with *T. aestivum* than in hybrids with tetraploid wheats, which conflicts with the data of PETO (1936). If *elongatum* does not have X_m, then it presumably carries a variant of the B genome, as suggested by STEBBINS and PUN, and has I_1I_2 in common with *intermedium*. This would be in accord with PETO's data, which, however, stand in need of confirmation with larger numbers of hybrid plants.

c. Triticum-Secale

Crosses between wheat and rye were among the first intergeneric combinations obtained, WILSON in 1876 having described wheat-rye hybrids. RIMPAU's (1891) wheat-rye amphiploid was probably the first fixed hybrid to be recognized as such (O'MARA, 1953).

The interest in rye has been largely a practical one, concerned with the possibility of making use of such rye characters as winter hardiness, disease and insect resistance, and low soil-fertility requirement. Two main types of endeavor have been involved, (1) attempts to obtain high-yielding amphiploids and (2) efforts to transfer rye characters to wheat.

a. Amphiploids

Although amphiploids have been made using many different varieties of wheat and rye, none has been reported which was fully fertile. The immediate cause of the infertility is apparently a reduction in chromosome pairing (LEISER, 1954), with most sporocytes having two or more unpaired chromosomes. Various suggestions have been made to explain the poor pairing:

1. The amphiploid chromosome number, 56, is too large to permit normal pairing. However, O'MARA's (1948) and NAKAJIMA's (1952) observations on wheat-rye amphiploids made using tetraploid wheats disprove this hypothesis. These 42-chromosome amphiploids also have irregular meiosis and are poorly fertile.

2. There is an unfavorable interaction between the hairy-neck chromosome of rye and chromosome IX of wheat. O'MARA (1947) showed that while the addition of a pair of hairy-neck chromosomes to wheat had a decidedly deleterious effect, reasonably normal plants were obtained when this pair was substituted for chromosome IX. This suggested that the poor performance of wheat-rye amphiploids might be due to a specific antagonism between the hairy-neck chromosome and chromosome IX of wheat. Accordingly, a nullisomic-IX amphiploid was synthesized (SEARS, unpublished). This amphiploid, with 27 pairs of chromosomes, was no more fertile or meiotically stable than control amphiploids with 28 pairs.

3. The genes that interfere with the easy crossing of wheat and rye may adversely affect the amphiploid (VON ROSENSTIEL, 1950). Amphiploids have been made, however, using Chinese Spring wheat (SEARS, unpublished), which crosses very readily with rye; and these amphiploids have not been highly fertile.

4. The genes for self-sterility of rye may have a deleterious effect when present in a plant which is self-fertilizing, as is the wheat-rye amphiploid (LEBEDEFF, 1934). Although it would require considerable experimentation to exclude this theory as a proper explanation for some of the results to be described under (5), the explanation given there seems more reasonable.

5. There may be recessive genes in rye that have an unfavorable effect when made homozygous, as they are in the amphiploid. MÜNTZING and AKDIK (1948) showed that inbred lines of rye tend to have reduced chromosome pairing and poor fertility. Evidently this is due to homozygosis of recessive genes unfavorable to chromosome pairing. Since these genes will also be made homozygous in the formation of amphiploids, they offer a possible explanation for the reduced chromosome pairing and fertility of wheat-rye amphiploids. MÜNTZING tested this possibility by producing wheat-rye amphiploids using inbred rye, from which most of the deleterious genes had presumably been eliminated. These amphiploids, which were exhibited in connection with the Seventh International Botanical Congress in 1950, were strikingly superior to control amphiploids in vigor and fertility. Whether full fertility will be reached by use of inbred rye remains to be seen, but the MÜNTZING approach seems to offer the greatest promise for progress in this direction.

β. Transfer of rye genes to wheat

VON ROSENSTIEL (1950) and O'MARA (1953) agree that none of the many efforts to transfer rye genes to wheat chromosomes has been successful. Success was claimed for some of the early attempts, in particular, but the possibility was not excluded of the characters' having come from other wheat varieties through contamination. Evidence has accumulated that the rye chromosomes pair rarely, if ever, with those of wheat, and this makes the possibility of a transfer remote. Nevertheless, there is some recent evidence of a transfer in a report by JONES and JENSEN (1954).

d. Triticum-Haynaldia

Although *Haynaldia* itself has not been crossed with common wheat, it has been possible to combine the chromosomes of the two species by using *T. dicoccoides* as a bridging species (SEARS, 1953b). The amphiploid *T. dicoccoides* × *H. villosa* was crossed with *T. aestivum* var. *vulgare*, and from this was derived a plant having 21 pairs of wheat chromosomes and 7 univalent *Haynaldia* chromosomes. Backcross offspring of this plant to wheat were studied by HYDE (1953), who succeeded in obtaining all seven addition monosomics.

B. Cytogenetics

1. Hexaploid wheats

a. Aneuploids

Common wheat, because it is a polyploid, is difficult to analyze genetically. Ratios often are multifactorial, and the large number of chromosomes makes the determination of linkages by ordinary means almost an impossible task. Recent work has shown, however, that advantage can be taken of the polyploid nature of wheat. Since every essential gene is present at least in duplicate, no chromosome is indispensable, and plants can be obtained that are completely deficient for each chromosome in turn (SEARS, 1954). These plants, called nullisomics, are extremely useful for indicating which genes are carried by each chromosome. Monosomics, trisomics, and tetrasomics have also been isolated for all 21 chromosomes, and these other aneuploids supplement the information provided by the nullisomics.

Aneuploids had been known in wheat for many years. The most intensive work had been done on the speltoid chromosome (see HUSKINS, 1946), but isolated occurrences of nullisomics for other chromosomes had been reported (THOMPSON, 1928; UCHIKAWA, 1938). KIHARA and MATSUMURA (see MATSUMURA, 1947) isolated a number of different nullisomics from a hybrid of *T. spelta* × *T. polonicum*. These of course involved only D-genome chromosomes; and being of hybrid origin, they did not give an unequivocal picture of the characteristics attributable to the nullisomes themselves.

The full series of monosomics, nullisomics, trisomics, and tetrasomics have been obtained in the variety Chinese Spring by SEARS (1939, 1944a, 1954). The first few monosomes and trisomes were found in the progeny of a haploid. Additional monosomes were provided by other haploids, but the major source of new monosomes was nullisomic III, which is partially asynaptic. Trisomes were also mainly obtained

Table 37. Some characteristics of the nullisomics of Chinese Spring wheat. R = reduced; MR = much reduced; I = increased; D = delayed; MD = much delayed

Homoeologous group	Chromosome	Height (Approx. % of norm.)	Tillering	Leaves		Culm diam.	Maturity	Fertility	
				Width	Length			Female	Male
1	I	80	R					+	+
1	XIV	50	R	R		R		+	+
1	XVII	50	R	R		R		+	+
2	II	45	MR	I	R	I	D	−	+
2	XIII	40	MR	R	R		D	−	+
2	XX	70	R		R			−	+
3	III	50		R	R			+	+
3	XII	70		R	R			+	+
3	XVI	40	R	MR	R		D	±	±
4	IV	60	R	R		MR		+	−
4	VIII	40	I	MR	R	MR	D	+	−
4	XV	60	R	R		R		+	−
5	V	70		R		R	D	+	−
5	IX	100		R		MR	D	+	−
5	XVIII	70	R	R		MR	MD	+	−
6	VI	50	R	R		R		+	±
6	X	60		R		R		+	−
6	XIX	70	R	R		R		+	+
7	VII	80						+	+
7	XI	80	R					+	+
7	XXI	80	R					+	+

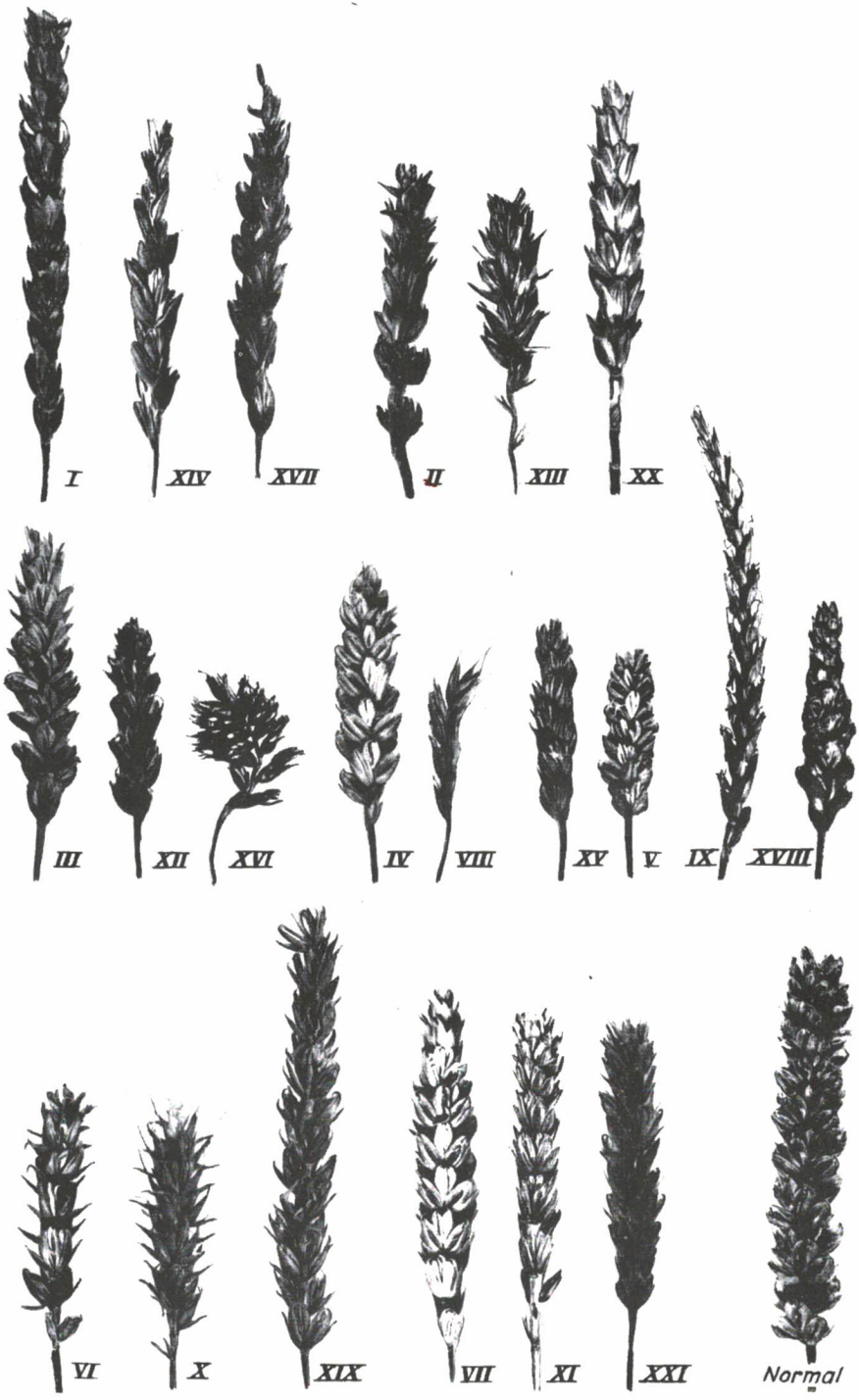

Fig. 27. Spikes of the 21 nullisomics of Chinese Spring wheat, grouped in accordance with the genetic relationships of the chromosomes concerned. X 3/4.

from the haploids and from nulli-III, but a triploid was utilized as the source of a few trisomes, and certain others appeared spontaneously in nullisomic lines, where they tended to compensate for the missing chromosome. The occurrence of trisomes in nullisomic lines has also been noted by HUSKINS (1941), and by KIHARA and MATSUMURA (see MATSUMURA, 1952b).

The chromosomes of wheat have been designated I to XXI, with XV to XXI being the chromosomes of the D genome. The speltoid chromosome is chromosome IX in this system.

Of the various types of aneuploids, the nullisomics are the most interesting. In nearly all cases the nullisomic differs more from normal than does the tetrasomic, the next most abnormal type. Also, the placement of a dominant gene on a particular chromosome is ordinarily revealed when that chromosome is completely absent. Although none of the 21 nullisomics (fig. 27 and table 37) is as vigorous or fertile as

Table 38. Frequencies of nullisomics and tetrasomics obtained from monosomics and trisomics, respectively, in the variety Chinese Spring (from SEARS, 1954)

Chromosome	No. offspring from monosomic	Percent nullisomic	No. offspring from trisomic	Percent tetrasomic
I	671	2.4	69	2.9
II	962	5.0	41	9.8
III	2682	7.6	96	1.0
IV	2159	6.4	78	3.8
V	1431	1.0	30	3.3
VI	598	2.5	39	2.6
VII	885	1.4	29	3.4
VIII	192	3.6	130	1.5
IX	832	3.4	—	—
X	1457	0.9	52	5.8
XI	331	3.3	34	2.9
XII	125	2.4	109	2.8
XIII	255	2.4	8	12.5
XIV	381	2.1	24	4.2
XV	1924	5.9	20	10.0
XVI	712	5.8	183	0.5
XVII	1109	2.4	69	1.4
XVIII	575	0.9	109	1.8
XIX	1084	2.8	8	12.5
XX	572	4.4	50	4.0
XXI	177	1.1	58	8.6

normal, all survive to maturity, and two, VII and XXI, approach the normal in appearance and fertility. Every nullisomic is fertile either as male or female or both. Nearly all are dwarfed in size, and most of them have narrow leaves and slender culms. Most monosomics and trisomics are difficult to distinguish from normal. The tetrasomics are generally morphologically distinguishable from normal, differing in the opposite direction from the corresponding nullisomics.

In transmission of whole-chromosome deficiencies and duplications from monosomics and trisomics (table 38), there is apparently no selection on the female side. On the male side, however, there is severe selection against pollen with either a missing or an added chromosome. For most chromosomes, but apparently not all, selection is stronger against gametes which are deficient than against those which carry the chromosome in duplicate. On the average, 20-chromosome male gametes have been

transmitted to only about 4.4% of offspring of monosomics, whereas about 7% of functioning pollen from trisomics has carried 22 chromosomes. The difference in ability of the two types to function is even greater than is apparent, for about 75% of pollen from monosomics has 20 chromosomes, as compared with only about 45% from trisomics having 22 chromosomes. The frequency of nullisomics obtained from the different monosomics has ranged from 0.9% to 7.6%, and of tetrasomics from trisomics, from 0.5% to 12.5%.

SEARS (1954) also reports obtaining either a telocentric or an isochromosome for one or both arms of each of the 21 chromosomes. It has been adequately shown by SANCHEZ-MONGE and MAC KEY (1948), SEARS (1952a), and MORRISON (1953) that these derivatives result from misdivision of univalents at either the first or second meiotic division.

Cytological studies of monosomes by MORRISON (1953) and SEARS (1954) have not been particularly rewarding. Distinct differences exist between the chromosomes both in total length and in relative length of arms, but there appears to be little chance of identifying more than a few of the chromosomes with certainty on the basis of cytological observations alone. The best stage for study is apparently second telophase, at which time the monosome is lagging and is relatively long. Of the three nucleolar chromosomes, one is clearly I, and MORRISON concluded that another is X.

The question of which of chromosomes I to XIV belong to the A genome and which to the B has not been answered, although LARSON (1952), from consideration of some genetic data, believes II to VII plus XIV to constitute the A genome. Insofar as this puts chromosome IX in the B genome, it accords with the findings of MATSUMURA (1952c), who came to this conclusion from cytological study of crosses between einkorn and mono-IX. LARSON's proposed grouping conflicts, however, with MORRISON's observation that two of the nucleolar chromosomes are I and X, for at least one of the nucleolar chromosomes must belong to the A genome. The evidence points to X as being this chromosome.

b. Homoeologous groups

By combining nullisomes with particular tetrasomes and observing in which combinations the tetrasome tends to compensate for the nullisome (SEARS, 1952b, 1954), it has been possible to place the 21 chromosomes into seven groups of three. Within each of these groups, which are called "homoeologous" groups (following HUSKINS, 1941) each tetrasome compensates, at least to some extent, for the other two nullisomes (with the possible exception of nullisome XVIII, for which critical data are not yet available). No certain case of compensation has been observed of a tetrasome for a nullisome of another group, although a considerable number of between-groups, combinations have been tested. The homoeologous groups are listed in table 37.

Each homoeologous group includes one chromosome from the D genome and presumably one each from A and B. It is a reasonable assumption that each group represents the derivatives of a single chromosome of the ancestral diploid species from which the three genomes evolved.

Within the homoeologous groups, the nullisomics tend to resemble each other. This, together with the fact that the homoeologous tetrasomes can cancel the effects of each nullisome, can only mean that the genes that are responsible for the characteristics of the nullisomic are duplicated on the other two chromosomes of the homoeologous group. Thus, the abnormalities exhibited by the nullisomics are not due to complete deficiency of genes but rather to reduction in dosage of certain genes from six to four. It is believed (SEARS, 1954) that these genes are relatively few in number.

The existence of the homoeologous groups indicates that translocations between chromosomes have not been frequent in the evolution either of the diploid species that combined to produce the allohexaploid or of the polyploid itself. It is difficult to see how the integrity of the groups could have been maintained in the face of many translocations. On the other hand, a few translocations exist between common-wheat varieties. Their existence without serious effect on the homoeologous groups can be explained by the fact that the nullisomic-tetrasomic compensation test measures only major homologies. Minor homology such as would usually be produced by interchange of a part of one chromosome arm could easily escape detection.

c. Genetic analysis

Many genes have been described in common wheat (see lists by AUSEMUS et al., 1946, and MATSUMURA, 1954). Most characters are due to two or more genes, however, with the result that the analyses have been difficult and therefore frequently of doubtful validity (VON ROSENSTIEL, 1950). Also, since no standard variety has been used for the genetic tests, the recorded results are mostly difficult or impossible to evaluate in terms of any single variety.

With the isolation of monosomics and nullisomics for all 21 chromosomes, a more satisfactory kind of analysis has become possible. In particular, the location of genes on individual chromosomes is relatively easy using the aneuploid material. This is being done in various ways (SEARS, 1953a):

1. It is ascertained that the effect of a particular gene is absent in a particular nullisomic. This method is applicable to genes present in the variety in which the nullisomics exist, provided that the gene has a different effect in zero dosage than at the level of two doses. Most dominants are included, and also certain recessives (the so-called hemizygous-ineffective recessives). A number of genes in the variety Chinese have been located using this method.

2. A cross is made with each of the 21 nullisomics, and the F_2 family that segregates abnormally is identified. In this family a dominant gene, instead of segregating 3 : 1, is present in from about 90% to 99% of the plants. Furthermore, only the nullisomics are recessive.

3. Disomic F_2 plants are selected and analyzed in the F_3 generation. Where the critical chromosome is involved, all the F_2 plants are homozygous for the gene concerned.

4. The individual chromosomes of another variety are substituted separately into a standard variety, and the resulting lines observed for differences from the standard. The substitutions are made by crossing and backcrossing to the respective nullisomics, using only monosomic plants in each generation. This method is particularly useful where segregation tends to be obscured in F_2, either by the action of modifying genes or by difficulties in making an accurate classification; and where tests may be required for a number of different characters, as for resistance to different diseases or to different physiologic races of a single disease organism. The method has the disadvantage, in common with method 1, that it shows only the total effect of the chromosome and therefore does not reveal whether the effect is due to a single gene or to more than one. Also, certain types of genes, particularly modifiers and complementary genes, are not susceptible to location by method 4.

One type of gene, the hemizygous-ineffective recessive, presents certain difficulties for nullisomic analysis. Three of these genes have already been described in wheat (SEARS, 1953b) out of only about twenty studied in detail. One, however, was the squarehead gene, which MAC KEY (1954a) has subsequently shown to be identical

with the speltoid-suppressing gene and frequently to be dominant rather than recessive. The hemizygous-ineffective recessives are simply genes which require two doses to reach their threshold of expression. The dominant alleles of the two thus far studied, virescent and sphaerococcum, show no dosage effect, behaving in fact like deficiencies. Hemizygous-ineffective recessives cannot be located by a simple F_2 test (method 2), because all disomics in the critical family are of recessive phenotype, and these occur in approximately the same 25% frequency as expected in all the other families. The determination can easily be made, however, by ascertaining in which F_2 family all of the recessives are disomic.

Table 39 lists the genes that have been located on particular chromosomes. In addition to those given, there are effects associated with various chromosomes, such as awn promotion by chromosomes II, XIII, and XX, which are probably due to single genes, but which cannot be identified as such because no non-promoting alleles are known at the loci concerned. LARSON (1952) has found effects of 11 different chromosomes on solidness of culm, but only four are listed in table 37, because only these four are definitely known to involve single genes. HEYNE and LIVERS (1953) noted effects of chromosomes XII, XV, XVI, and XXI on awn development, but did not prove that single genes were involved. SEARS and RODENHISER (unpublished) have found chromosomes VI of Red Egyptian and VIII of Hope to carry stem-rust resistance, but whether a single gene is involved in each case has not been determined.

A type of analysis that has many of the advantages of nullisomic analysis, but is applicable only to genes on D-genome chromosomes, is based on the study of 29-chromosome plants derived from hexaploid-tetraploid crosses. These are D-genome addition monosomics, and genes are revealed by their effects in particular additions and lack of these effects in the 28-chromosome offspring. YAMASHITA (1947) identified several characters with particular chromosomes in this way. MATSUMURA (1952a), who calls the 29-chromosome plants "D-haplosomics", studied some of the same characters to determine which of his nullisomics corresponded with the addition monosomics responsible for the characters. The chromosomes concerned are apparently XVII for procumbent tillering, XIX for lax spike and short outer glume, and XX for hollow stem. It is not clear, however, that single genes are involved in each case, except for hollow stem, which LARSON (1952) has independently shown to be due to a gene on chromosome XX.

Requiring some explanation is the squarehead, non-speltoid gene on chromosome IX. Its effects were long believed to be due to two different genes located about 65 crossover units apart, but MAC KEY (1954a) shows that this conclusion involves a misinterpretation of the genetic data. He believes that the two effects are due to a single gene Q, since the radiation-induced mutations he obtained in a squarehead, non-speltoid variety were always to non-squarehead speltoid. Although most non-squarehead varieties are non-speltoid, the non-squareheadedness is attributed to modifying genes rather than to any difference in effect of Q. Q has frequently been considered recessive, but in some crosses the heterozygote is more nearly non-speltoid than speltoid. The genes for speltoid and *spelta* are held by MAC KEY to be identical, any differences in expression being due to modifying genes.

Of the 29 genes listed in the table 39, five are located on chromosome X, five on IX, three each on III, XVI, and XX, and two each on VIII, XI, and XIX. Although most of these have not been checked for linkage intensity, crossover values are known for some of the genes on chromosomes IX. The squarehead gene, Q, is about 30 units distal to the awn suppressor, B_1 (see MAC KEY, 1954a), and the pubescent node gene is located about 5 units on one side or the other of B_1 (GAINES and CARSTENS, 1926).

Table 39. Genes known to be located on a particular chromosome

Chromosome	Gene concerned	Symbol	Authority	Variety
I	Brown glumes		UNRAU (1950)	Federation 41
III	Desynapsis		H. W. LI (priv. comm.)	Varietal hybrid
	Neatby's virescent	v	SEARS (1954)	Varietal hybrid
	Necrotic leaves		SMITH (in SEARS, 1954)	Pilot (A-bomb)
VIII	Hooded (awn inhibitor)	Hd	SEARS (1944a)	Chinese
	Solid-stem promoter		LARSON (1952)	Chinese
IX	Squarehead, non-speltoid	Q	SEARS (1944a)	Chinese
	Awn suppressor	B_1	UNRAU (1950)	Hymar
	Pubescent nodes		SEARS (1944)	Chinese
	Winter habit of growth		UNRAU (1950)	Hymar
	Basal sterility of speltoid	G	FRANKEL and FRASER (1948)	Yeoman II
X	Awn suppressor	B_2	SEARS (1944)	Chinese
	Stem-rust resistance 1		SEARS a. RODENHISER (1948)	Timstein
	Stem-rust resistance 2		SEARS a. RODENHISER (1948)	Timstein
	Leaf-rust resistance (seedling)		HEYNE a. LIVERS (1953)	Pawnee
	Leaf-rust resistance (adult)		UNRAU (priv. comm.)	Chinese
XI	Red coleoptile		SEARS (1954)	Hope
	Mildew resistance		SEARS a. RODENHISER (unpublished)	Axminster
XIII	Solid-stem inhibitor		LARSON (1952)	Chinese
XIV	Pubescent glumes		SEARS (1954)	Indian
XVI	Red seeds		SEARS (1944)	Chinese
	Sphaerococcum effect		SEARS (1947)	*T. aestivum sphaerococcum*
	Bunt-resistance modifier		UNRAU (1950)	Chinese
XVIII	Winter habit of growth		JENKINS a. KUSPIRA (priv. comm.)	Kharkof
XIX	Solid-stem inhibitor		LARSON (1952)	Chinese
	Stem-rust resistance		SEARS and RODENHISER (unpublished)	Thatcher
XX	*Compactum* (club) spike	C	UNRAU (1950)	Hymar
	Solid-stem inhibitor		LARSON (1952)	Chinese
	Stem-rust resistance		SEARS and RODENHISER (unpublished)	Red Egyptian

MAC KEY (1954a) notes that the gene S_K on IX for spring habit (presumably the same as the gene identified by UNRAU) is located proximally to B_1. The two genes on X for stem-rust resistance are linked with about 30% crossover, according to the data of SEARS and RODENHISER (1948).

A few linkages involving genes not listed in table 37 are reviewed by SEARS (1948).

d. Mutation

Mutations have been observed in hexaploid wheat by many different workers. Almost all of these mutations have been of a single type, speltoid. As HUSKINS (1946) showed, and as amply confirmed by MAC KEY (1954a), this mutation involves loss or change of a particular gene on chromosome IX. This gene, previously designated variously as k, S, and q, is labeled Q by MAC KEY (1954a) in his definitive analysis of the speltoid problem. It has a pleiotropic action, affecting particularly density of spike, and size, shape, nervation, coloration, and keel-development of glume. In certain varieties it also determines the fertility of the basal florets of the spikelets. The speltoid mutation occurs spontaneously in pure-line material in appreciable numbers. In a carefully controlled experiment MAC KEY found 0.6 to 0.7% speltoids, a frequency which agrees well with that obtained by numerous other workers in somewhat less precise studies.

Speltoid is not the only mutant occurring spontaneously; in fact, MAC KEY found 10 lax-spiked types and only 8 speltoids among 21 spontaneous mutants. The lax-spiked mutants are more difficult to identify, however, and thus have not ordinarily been reported in such high frequency.

In varietal hybrids, mutations occur in frequencies that may be many times as high as in pure lines. MAC KEY calculated from the data of KAJANUS a speltoid mutation frequency of over 50% in some crosses.

FRANKEL (1950) reported the occurrence of a chlorophyll defect, *striato-virescens*, in the F_2 generation of a varietal cross. This character depended upon three recessive, complementary genes. Evidence was presented that the three genes had arisen simultaneously, probably in the somatic phase.

Speltoid mutations induced by X-rays and neutrons show a "pronounced conformity" with those occurring spontaneously, according to MAC KEY (1954a). He divided the speltoids into three groups according to the amount of deficiency involved: (1) beardless-deficient speltoids, in which the B_1 locus about 30 units proximal to Q has not been lost; (2) bearded-deficient speltoids, in which B_1 but not the whole chromosome has been lost; and (3) monosomic speltoids, in which the entire chromosome IX is gone. Thus group 1 consisted of small losses or point mutations, and the other two groups of relatively large losses. Of 172 spontaneous mutants observed in a pure line, 98.8% involved large losses, 59.9% being monosomic. In wide varietal crosses (KAJANUS' material) large losses also were involved in 98% of the 102 speltoid mutations, but only 5.9% were monosomic. Induced mutants included more short deficiencies, 9.4% from X-rays and 5.2% from neutrons, and were intermediate to the spontaneous mutants in pure-line and hybrid material in respect to the relative frequency of the two kinds of large losses (17.9% and 25.6% monosomic from X-rays and neutrons, respectively).

MAC KEY induced a total of 1949 mutants, of which 35.0% were lax-spiked, 28.3% speltoid, 19.7% dense-spiked, 14.1% short-strawed, about 27.8% awned,[1]) about 24.5% of winter habit[2]) and 0.2% chlorophyll-defective. Other mutants which appeared in small numbers, usually or always in combination with one of those already listed, were: decreased waxiness, increased waxiness, pseudo black-chaff, false foot-rot, bearded lemmas, delayed ripening, early ripening, and spring habit (in Scandia III).

As MAC KEY points out, there is good reason to believe that all or nearly all of the mutations observed were due to deficiencies, or to duplications resulting from non-disjunctional segregation from reciprocal-translocation complexes, rather than to intragenic changes. Some were clearly deficiencies for known genes. The speltoid mutants were all or nearly all losses involving the gene Q on chromosome IX; the awned mutants were due to deficiencies for the awn suppressor B_1 on chromosome IX; and the winter-type mutants were due to loss of the gene S_K, also on chromosome IX.

A striking difference between results with hexaploid wheat and with einkorn, barley, maize, and other diploid plants has been the virtual absence of chlorophyll-defective mutants from both spontaneous and induced classes in the hexaploid material. This difference is all the more impressive in view of the fact that the total number of mutants

[1]) In MAC KEY's table 4, only 1.3% of the mutants are listed as bearded. As shown in his table 10, however, 93.5% of a large sample of induced speltoid mutants also were awned.

[2]) On page 151, MAC KEY mentions winter-type mutations in Rival amounting to only 1.05% of the total observed for that variety. According to personal communication, however, up to 82.9% of the sample of induced speltoids were also of winter-type. (Homozygotes were not obtained for 108 of the deficient speltoids, and very probably the large majority or all of these would have been both bearded and of winter habit).

obtainable by the use of radiation is larger for the hexaploid than for the diploids. MAC KEY (1954a) recovered 1.67 mutants in wheat per N_2 progeny from his highest dosage of neutrons — more than three times the frequency he found obtainable with barley.

The absence of chlorophyll-defectives and other "vital" mutations in the hexaploid is explained by MAC KEY in the following way: Essential genes, such as those for chlorophyll production, cannot be lost or greatly modified in the diploid, since this would be lethal. Hence, all such genes are duplicated in the formation of amphidiploids, and subsequent loss or mutation at one locus is masked by the presence of the duplicate locus. Genes for non-essential ("peripheral") characters, such as awn development, shortening or lengthening of spike or culm, and earliness of maturity, tend to be modified during the evolution of diploids; and when the diploids are then combined into a polyploid, these genes are not present in duplicate, and their loss results in phenotypic changes. Since the polyploid tolerates loss mutations to a much greater extent (even whole-chromosome losses in hexaploid wheat) than does the diploid, the total number of mutations recoverable is significantly greater in the polyploid.

That each gene essential for chlorophyll production and other vital characters is present at least in duplicate in hexaploid wheat is clearly shown by the nullisomics (SEARS, 1954), none of which is defective in chlorophyll, and all of which are viable to maturity and partially fertile. The other half of MAC KEY's assumption — that the mutants which do occur involve the loss of genes whose covering loci have been lost during evolution — may not be entirely correct. The speltoid, awned, and winter-type mutants are of this type; but other mutants, particularly some of those with lax spikes or short straw, may owe their effect to a mere reduction in dosage in a triplicated series rather than to loss of an independently effective gene. There is evidence from the nullisomics and from various compensating nullisomic-tetrasomic combinations that dosage reduction at the 6 to 4 level can lead to phenotypic effects. The critical test for mutants of this type would be that apparently identical mutants would give a mutant F_1 when crossed together, but in F_2 might segregate both normals and extreme mutants.

Since most of MAC KEY's mutants were deficiencies, consideration of the characteristics of the nullisomics should give some idea regarding which chromosomes carry the mutants. These is a source of error in this, however, in that the mutants occurred in the Swedish varieties Scandia III and Rival, whereas the nullisomics are present in Chinese Spring. Particular characters may be determined by different genes or combinations of genes in the different varieties; for example, awnlessness is due to a gene B_1 on chromosome IX of the Swedish varieties and to B_2 on chromosome X and Hd on VIII of Chinese Spring. Actually, about half of MAC KEY's mutants are attributable, as he shows, to aberration of chromosome IX. Included among these are speltoid, awned, winter habit, and about half the dense-spiked mutants (duplications for Q). The lax-spiked mutations would be suspected of occurring in chromosomes I, XIV, XVII, or XIX. The half of the dense-spiked mutants not due to duplications of Q seem most likely to involve losses of genes on chromosomes III, XII, or XVI. The spring-type mutants obtained in Scandia III could be due to loss of part of chromosome XIX, a chromosome which in Chinese Spring carries a gene or genes for late maturity. The short-strawed mutants are difficult to locate even tentatively, because of uncertainty as to which nullisomics are dwarf because of deficiency of specific genes for length, and which are dwarf because of general lack of vigor. The most conspicuously dwarf nullisomics are II, III, VI, VIII, XIII, XIV,

XVI, and XVII (table 37). The chlorophyll mutations cannot reasonably be explained as simple deficiencies, unless the Swedish wheats differ significantly from Chinese in their chlorophyll genes, for no nullisomic in Chinese is chlorophyll defective. At least one of the genes, masculescens in Scandia III, is simply inherited. Perhaps this gene is like NEATBY's virescent in being actively inhibitory of chlorophyll formation.

Mutations involving genes on chromosome IX are almost as frequent as all other mutations combined, according to MAC KEY's findings. In part this is attributable to the fact that the genes whose loss leads to striking, easily identifiable effects, *vulgare* (Q), awn suppressor (B_1), and spring habit (S_K), were all located on chromosome IX in MAC KEY's varieties. In the variety Chinese the awn mutants would have occurred on chromosomes VIII and X instead of IX.

Since there is no obvious reason why there should not have been as many whole-chromosome losses involving each of the other 20 chromosomes as there were of IX, it may be assumed that these did in fact occur. Their total must have been large, for 25.6% and 17.9% of the total of the speltoids obtained from neutrons and X-rays, respectively, were monosomic-IX mutants. Almost all of the monosomic mutants involving other chromosomes would have been easily recognizable when made homozygous (i.e., nullisomic), and, indeed, even deficiencies for part of one or the other or either arm of most of the chromosomes would presumably have had a very appreciable phenotypic effect when homozygous.

An explanation for the poor representation of mutants involving other chromosomes than IX is perhaps to be found in the difficulty of recognizing monosomics for these other chromosomes, and in the low frequency of nullisomic offspring produced by the monosomics. In populations of the size used, most of the monosomic mutants would presumably have failed to yield any nullisomics, and hence would have gone undetected. Losses of a large part of one arm might also have given a low frequency of homozygotes in many cases. Where chromosome IX was concerned, deficiency for Q was recognizable when heterozygous (or hemizygous), and thus all the monosomics and long-arm terminal deficiencies (Q lies near the distal end of this arm) presumably were identified.

Only one of MAC KEY's mutants, a spontaneously arisen awned type, excelled the parental variety in yielding ability. As he points out, however, the mutants tested were all selected because of morphological effects, and this is not the most efficient method of looking for mutations to increased productivity. Both MAC KEY (1954c) and SEARS (1954) argue that beneficial mutations should be more frequent in a polyploid such as wheat than in a diploid. Most of the genes in a hexaploid are triplicated, and it is unreasonable to assume that a dosage of six is optimum in every case; the optimum may just as well be four in some cases. In these cases, loss of one locus would be beneficial. Certainly some genes have an increasing effect at dosage levels up to and beyond six. Dosages greater than six are clearly beyond the optimum for many of the genes of wheat (hence the inferiority of tetrasomics as compared with normal), and even six may well be too high for some. If hexaploid wheat were an old species, mutation and selection should already have reduced the dosage of each gene to the optimum; but the species is actually very young.

2. Diploid wheats

Because the diploid wheats are of small agronomic importance, they have received relatively little attention from cytologists and geneticists. SMITH (1936, 1939, 1942) however, described a collection of 56 mutants, mostly radiation-induced. These mu-

tants were largely chlorophyll deficiencies and morphological abnormalities, but included several types with aberrant chromosome behavior. SMITH established six linkage groups.

More recently KIHARA and his colleagues have also undertaken a cytogenetic analysis of einkorn. YAMASHITA (1951) has obtained reciprocal translocations involving all seven of the chromosomes, and has combined these to produce a plant with a ring of 14 chromosomes. KIHARA and YAMASHITA (1954) list 36 mutants obtained. By means of the reciprocal translocations, at least one gene has been located on each of the seven chromosomes.

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