H. Kihara : Genome-Analysis in *Triticum* and *Aegilops*. X. Concluding Review^{1, 2}

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Cytogenetics of species hybrids and studies on polyploidy developed rapidly in the last three decades into a new branch of biology. Their theoretical and practical aspects seemed from the very beginnings to offer unlimited possibilities, and natural as well as artificial polyploids became the subject of great interest to plant geneticists in many countries.

Kihara's investigations of the karyogenetical relationships between the three wheat groups—Einkorn, Emmer and Dinkel—started in 1918 (Kihara, 1919). Then, in 1924, followed his well known, classical studies on the pentaploid hybrids, with many interesting sidelights, like his observations of viable, fertile 20-bivalent descendant's (Sears' nullisomics).

The relationships between the three genomes—A, B and D—having been laid clear, Kihara decided to include in his further investigations other groups of *Triticinae* and started with a few available species of *Aegilops*. The results of the first studies were published in 1929, upon which, starting with 1930, followed a series of contributions under the headline “Genomanalyse bei *Triticum* und *Aegilops*” (1930–1949).

In the first contribution (I, 1930) Kihara formulated a biogenetical definition of genome and laid down a broad foundation for his genome-analysis with his “Analysatoren-Methode” which proved to be very helpful in ascertaining the genomes of polygenomic plants of unknown genomic constitution.

Between the years 1930 and 1936 followed, with short intervals, five more contributions. During the troubled times later, until 1949, only three further reports were published (VII–IX). But experimental work was going on, as well as it was possible under the circumstances, and a number of important separate reports, closely connected with the analysis of genomes, were published by Kihara (to a great extent in Japanese) and various members of his institute. Also, during these years, a considerable amount of additional information was provided by the more fortunately situated plant geneticists of America who developed

¹ Contributions from the Laboratory of Genetics, Biological Institute, Kyoto University, No. 208.

² Contributions from the National Institute of Genetics, Japan, No. 18.

a great activity on similar problems and produced a real display of outstanding achievements like those of Sears.

The most important results of the investigations carried out by Kihara and his collaborators were 1. the clearing up—along the main lines—of cytogenetical relations in the *Triticum-Aegilops* group and 2. the establishing of a new systematics of *Aegilops*, based on the genome constitution of its species—the first attempt to classify a genus on the basis of genomic relations.

In the belief that the pioneering genome-analytical work in wheat and *Aegilops*—as far as Kihara's programme is concerned—can be considered as concluded, we wish to bring the series to an end with this last contribution which will give a brief account of the most important results.

I. Definition of Genome and Genome Homologies

Winkler was the first to use the term "genome" (1920). He called a haploid chromosome set genome. According to Kihara a genome, as represented by a chromosome set, is a fundamental genetical and physiological system whose completeness as to the basic gene content is indispensable for the normal development of genes in haplo- and zygotes in diplophase. Consequently, at least one pair of complete, homologous genomes must also be present in a fully viable and to a certain degree fertile polyploid, while the remaining complement may suffer changes or deficiencies which could not be tolerated in a diploid.

Two genomes are strictly homologous, if the pairing chromosomes are identical as to the linear gene arrangement and freely interchangeable which guarantees genomically conditioned full fertility.

Two genomes are semihomologous, if all or a part of their pairing chromosomes have only similar segments in common. On the amount of segmental similarity depends the amount and manner of pairing and the herewith conditioned fertility.

Strictly non-homologous genomes did not occur in our group which probably holds true also for other groups of intercrossable species. In absence of the homologous partner all of the examined genomes were at least weakly interrelated, showing besides unpaired chromosomes a very variable number of loosely connected bivalents.

II. Principles of Genome-Analysis

A. *The analysers.* Kihara's "Analysatoren-Methode" is based on the use of diploid analysers in crosses with polyploids whose genome content has to be ascertained. The first thing, of course, is the investigation of the pairing relations between the genomes of all available diploid species of the group in question. This can be done by bringing

their genomes—so to speak—face to face with each other in all possible hybrid combinations. The examination of the first metaphase and fertility gives an insight into the genomic relations of the future analysers.

In our case, only in the course of many years could almost all diploid *Aegilops* species be assembled in the Kyoto collection. Two species proved to be of varietal rank, namely *Ae. Heldreichii* (variety of *Ae. comosa*) and *Ae. Aucheri* (variety of *Ae. speltoides*)¹. The hybrids between all other species showed a wide range in semihomologous chromosome pairing and a more or less defective fertility which varied between 0 and ca. 6%. On the basis of these two features Kihara divided the diploid species into the three following groups, characterized by a considerable amount of semihomologous pairing and corresponding scant fertility within the groups and only very few affinities between them.

1. *Ae. caudata* (C genome) and *umbellulata* (Cⁿ genome).
2. *Ae. comosa* (M genome), *uniaristata* (Mⁿ genome), *mutica* (Mt genome) and *squarrosa* (D genome).
3. *Ae. speltoides* (S genome), *longissima* (S^l genome) and *bicornis* (S^b genome).

Through this preliminary investigation the nine diploid species were established as the analysers (comp. Table 5, p. 116).

B. Analysis of genome constitutions in polyploids. With the analysers at hand, the search for corresponding genomes in the polyploids can be started with the establishing of hybrids between them and examination of the meiotic behavior and fertility.

It will be referred in this chapter only to allopolyploids, as in nature only such occur in our group.

In order to illustrate the procedure, a hypothetical case will be considered first. Schema 1 represents an extreme case, never met with in nature, but very convenient for the explanation of Kihara's working methods. We assume that the given allotetraploid², placed in the middle of the triangle, has the genome constitution AABB and x chromosomes in a haploid set. How will it behave in crosses with 1) AA and BB and

Schema 1. Hypothetical case with no affinities between the involved genomes. Explanation in text.

¹ Also *Ae. sharonensis* can be considered to be a variety, of *Ae. longissima* (Kihara and Tanaka, unpubl.)

² The question of deciding between auto- and allopolyploidy will be treated later. The term amphidiploid will be used only for artificially produced allopolyploids.

2) in crosses with other diploids, for instance CC. Between the analysers A, B and C no relations are supposed to occur, i.e. the hybrids between them should show $2x$ univalents. It is evident from Schema 1 that AABB crossed either with AA or BB will produce at metaphase $x_{II} + x_I$, and with CC and all other analysers $3x$ univalents. From these premises follows that any tetraploid of unknown genome constitution has to be crossed with diploid analysers, until two are found which give at metaphase the same configuration, i.e. $x_{II} + x_I$. These two are the components of the given allotetraploid. All hybrids with other analysers would show only univalents. A final proof, interesting also from the phylogenetical point of view and made easy through the use of colchicine, would be to synthesize artificially AABB from the cross $AA \times BB$. Should the amphidiploid obtained from this cross correspond in every respect with the original AABB, then its parents could have been only the two analysers, AA and BB, or some other varieties of the two species.

When we rise to higher levels of polyploidy, the same methods can be applied with self-evident modifications.

Let us now consider concrete cases, solved by Kihara and other investigators.

1. *Aegilops cylindrica* ($2n=28$) and other tetraploids. Let us assume that both genomes are not yet known and designate them as X and Y. The first step would be to cross *cylindrica*, XXYY, with all available 10 analysers (9 *Aegilops*- and 1 of the Einkorn species). As Schema 2 shows, our postulates as to affinities of Schema 1 had to be changed according to our findings. At least 8 of the 10 analysers should prove as nonhomologous or partly semihomologous with X and Y, and the hybrids should show no pairing or a few loosely associated bivalents, which is usually the case. Should we be fortunate enough to have the two species which constitute *cylindrica* among our analysers, then only these two would produce in crosses with *cylindrica* 7 close bivalents and 7 univalents which would prove beyond doubt their identification with the components of *cylindrica*. We know now that the two diploid species for which the search was going on are *Ae. caudata* (C-genome) and *Ae. squarrosa* (D-genome); we also know that they should give from the

Schema 2. *Ae. cylindrica* case. *ca*=*caudata*, *sq*=*squarrosa*, *ei*=*einkorn*. 7 closely connected bivalents are formed in the hybrid *cylindrica* $\times$ *caudata*. All other bivalents are loosely associated.

cross CC × DD the artificial amphidiploid *cylandrica* and that such a plant was really produced. But was this the factual procedure in Kihara's investigation of *Ae. cylandrica*? The answer is: no. At first a hybrid of *Ae. cylandrica* with *T. vulgare* was made by Sax and Sax (1924). The observed 7 close bivalents were interpreted by the authors as being caused by the homology of one of the three *vulgare* genomes with one of the two *cylandrica* genomes. As soon as *Ae. cylandrica* was received in the Kyoto collection, Kihara repeated the cross and found a similar meiotic behavior in the hybrid. Also, his investigation of the hybrid between *Ae. cylandrica* and Emmer showed that the genome in common in *T. vulgare* and *Ae. cylandrica* could be only the Dinkel genome, D (1931). With these results Aase's (1930) conclusion, that *Ae. cylandrica* has the third *vulgare* genome, was fully confirmed.

On taxonomic grounds, Kihara did not believe that *Ae. cylandrica* could have played a role in the origin of *vulgare* wheats and carried out a systematical series of crosses with the diploid analysers. One of them, with *Ae. caudata* (genome C), gave the clue to one of the *cylandrica* components (Schema 2), but the other was still missing. Kihara assumed on the ground of morphological features that only *Ae. squarrosa* could be the missing species (DD). But all attempts to cross *cylandrica* with this analyser ended in failure. Finally, Kihara crossed *Ae. caudata* with *Ae. squarrosa* and obtained F₁ plants which could not be distinguished from *Ae. cylandrica* (1939). This proved, indirectly, that he was right in assuming that *Ae. squarrosa* might have the Dinkel genome. The corresponding amphidiploid was later obtained by Sears (1941); it resembled in every respect *Ae. cylandrica*. In the meanwhile a member of Kihara's institute (Kondo, 1941) repeated the cross, this time successfully, between *Ae. cylandrica* and a tetraploid *squarrosa* obtained with colchicine, with the expected result as to chromosome pairing in the hybrid. Thus, all links necessary to make the proof conclusive were at last furnished. Kondo's instructive experience showed that when crossability cannot be obtained in diploid condition, the cross may succeed with the corresponding tetraploid. This device was later very often used with success. In this way, after many years of pioneering work the genome constitution of *Ae. cylandrica* was at last ascertained and, at the same time, the diploid holder of the D genome was found. Should Kihara have had at the same time *Ae. cylandrica* and the required analysers, with the help of colchicine the problem could have been solved in one or two years.

In a similar way the genome constitution of *Ae. triuncialis* was resolved into its components, the genomes C and C", and again synthesized from the cross *Ae. caudata* × *Ae. umbellulata*. An interesting shortcut was taken by Matsumoto and Kondo (1942) who crossed *Ae. squarrosa*

(genome D) with *Ae. uniaristata* (genome M^u) and produced an amphidiploid very similar to *Ae. ventricosa*, which consists of genomes D and M^v (another modification of M).

Let us consider *T. Timopheevi*, another tetraploid analysed by us. Here, our findings were not published before the total results had been established beyond any doubt, which required a legion of various, direct and indirect, crosses. *T. Timopheevi* was found in Georgia and was placed by Zhukovsky, one of the most notable wheat systematicists, in the Emmer group as closely related to *T. persicum*. As soon as it was received by us, it was crossed with all available Emmer wheats, including *T. persicum*, and also with Einkorn and Dinkel. Also all other analysers and tetraploid *Aegilops* species were used in crosses. At the same time, for comparison's sake, the Emmer wheats of our collection were combined with each other in 20 crosses. We found (1934) that *T. Timopheevi* has the A genome in common with the three known wheat groups. But we could not identify the second *Timopheevi* genome, which evidently is not shared with any of our wheat and *Aegilops* species. We designated it by the letter G (Georgia) and added a new wheat group¹, the *Timopheevi* group, to the three already known. The numerous simultaneously carried out intra-Emmer crosses brought the expected results, namely regular chromosome pairing and good fertility, except for sporadic occurrence of univalents or tetrapartites.

Neither could the B genome, quite surely different from G, be identified with any one of our living genome collection.

2. *The hexaploid vulgare wheats.* The most important plant in our whole group is of course *T. vulgare*, the bread wheat, which always stood in the center of universal interest. The number of chromosomes in the three wheat groups was established as early as 1918 by Sakamura (Sax determined in the same year the chromosome number of *T. durum*). The crosses between the groups (Kihara, 1919 and 1924) showed that the Einkorn genome was common to all three groups, further that both Emmer genomes were shared by the Dinkel group. The Dinkel genome, D, remained isolated until it was identified with one of the *cylindrica* genomes by Aase (1930) and Kihara (1931). But it took more than three decades to find that *Ae. squarrosa* too has the genome D and, also, that it must have contributed this genome to the make-up of *vulgare* (or *spelta*) in a natural cross with one of the Emmer wheats. This was proved by McFadden and Sears (1944) through the synthesis of artificial *T. spelta* obtained from the cross between *T. dicoccoides* and *Ae. squarrosa*. In the same year Kihara (1944) made known that he arrived indirectly at the same conclusion as to the

¹ The "Gordian knot" which we are supposed to have cut according to Dobzhansky (1941) was in fact very painstakingly unraveled.

origin of *T. vulgare* on the grounds of a genomic and morphological analysis.

The assumption that the species *squarrosa* is really one of the parental species of Dinkel wheats is strongly supported by plant-geographical considerations (Kihara and Lilienfeld, 1949). The investigation of the constitution of *T. vulgare* shows that genome analysis can play an important role in the solving of phylogenetical problems in plants, with the help of additional informations from related other branches of botanical sciences.

3. *The octoploid Aegilotriticum*. The analysis was carried out with Tschermak's *Aegilotriticum* (Bleier, 1926). This octoploid was produced from the cross *Ae. ovata* $\times$ *T. durum*. The parents being known, it was a suitable material for the demonstration of Kihara's working methods. The analysers in this case were 1. *Ae. ovata* (CⁿCⁿM^oM^o) and, in place of the other parent, another Emmer wheat, *T. dicoccoides* (AABB), and 2. *T. spelta*, with the *vulgare* genome complement, AABBDD. The genomic formula of *Aegilotriticum* is: CⁿCⁿM^oM^oAABB. At the metaphase of the hybrid with AABB mostly 14_{II}+14_I were observed; sometimes tripartites could be seen, as a result of semihomologous pairing of genomes A and B with the other genomes. The hybrid with *Ae. ovata*, CⁿCⁿM^oM^o, showed a similar meiotic behavior. The last hybrid, with *T. spelta*, AABBDD, showed at metaphase mostly 14_{II}+21_I.

Thus, all three combinations showed exactly the expected results. The investigation of the genomic constitution of *Aegilotriticum* may serve as a model of Kihara's procedure.

4. *The pentaploid hybrids*. The investigation of these hybrids (1919, 1924) gave an early start to Kihara's genome-analysis.

The pentaploid hybrids were won from crosses between Emmer- and *vulgare* wheats. Consequently, their genome constitution is represented by the formula AABBDD. Species hybrids of this nature were considered up to that time to behave quite irregularly in the further generations. Kihara (1924) found the pentaploid wheat hybrids to follow definite rules which he derived from the chromosome combinations in F₂. On their basis he divided the F₂ offspring in two groups: 1. "fertile" and 2. "sterile" chromosome combinations. The first group was further subdivided into a) the chromosome numbers decreasing group ("Verminderungsgruppe") and b) the chromosome numbers increasing group ("Vermehrungsgruppe"). The first has 28-34 somatic chromosomes and at metaphase the configuration 14_{II}(7 AA+7 BB)+0_I-6_I from genome D. The 29-34 chromosome plants revert soon in the course of further generations to the Emmer type with 14_{II}, i.e. AABB, when all the univalents of the incomplete genome D have dropped out. The increasing group, with 36-42 somatic chromosomes, consists of plants which

possess all elements of D, double or single. This group, when bred further, reverts slowly to the 42 chromosome type, AABBD, by acquiring in the process of fertilization the missing partners of the D complement. Thus, further generations of the pentaploid hybrids and, in general, all hybrids of the genome pattern AAB (i.e. with one or more pairs of homologous genomes + one or more single genomes) return to the parental genome types, wherewith the development is brought to a stop, and cytological and, eventually, genetical constancy is established. The "sterile" chromosome combinations can never revert to the parental types and, with a few exceptions, die out.

Kihara set himself the task of investigating the particulars of the development in both groups, the increasing and decreasing. He attacked the problem at the source—starting with the examination, in very large numbers, of the chromosome combinations in the sporocytes of F_1 . He wanted to obtain a material large enough for the comparison of their factual frequencies with the theoretical figures. This was done in a direct study of meiosis, mostly in the microsporocytes, in F_1 , and indirectly in two series of backcrosses, namely 1. the so called "Aequationskreuzungen", i.e. $F_1 \times$ parents (AABBD $\times$ AABB and AABBD $\times$ DD) and 2. "Zertationskreuzungen", i.e. parents $\times F_1$ (AABB and AABBD $\times$ AABBD). The purpose of the first series was to explore the distribution of the various chromosome combinations in the macrosporocytes of the hybrid and to ascertain the fitness of the corresponding gametes. The object of the second series was to examine these conditions for the microsporocytes. The obtained ratios were not in good accord with the theoretical figures, calculated on the basis of a random distribution of univalents. The search began for the causes of the disagreement. The first clue gave the fast development of the decreasing group back to AABB from which an elimination of univalents could be inferred, and calculations have been worked out to determine the degree of elimination. But even then discrepancies remained, also unexplained differences between the reciprocal crosses added to the intricacy of the situation. A whole complex of disturbing factors was found to be responsible, as can be seen from the twelve successive contributions of the series (Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde, I–XII; Kihara et alii/I–IV/, Matsumura/V–XI/, Kihara and Matsumura/XII/). They had to be disposed of, one after another, before the situation was laid clear. Only a few points shall be mentioned, as it is not possible to go into full particulars in this survey:

1. Elimination of univalents plays an important role.
2. Moreover, the univalents are distributed not separately but in bunches.
3. Strong competition between the pollen grains, those with 14 and

21 chromosomes being the fittest.

4. Selective fertilization does not occur, provided that enough pollen is furnished. If not, the embryosacs with intermediate chromosome numbers fail to be fertilized which may become a disturbing factor.

5. Poor seed germination was observed when Emmer was the mother, caused by a greater disproportion in the endosperm between the quantities of the genomes AB and D in this direction of the cross than reciprocally, namely 3AB: 1D and 3AB: 2D, respectively.

6. Zygotic elimination of the "sterile" combinations occurs,—and so forth.

A very laborious investigation of the distribution of chromosome combinations in a large F_2 was carried out by Kihara and Matsumura (1940). When all the disturbing factors were taken into consideration, the frequency of the chromosome combinations obtained from the F_2 investigation could be brought into agreement with the results of the other experiments and with the theoretical expectations. Also, the differences between the reciprocal crosses could be explained.

The "sterile" combinations were represented by weak, sterile plants, with the exception of healthy dwarflike individuals with 20 bivalents and fairly good fertility. At first four different dwarfs were found; in each of them another chromosome pair of the D genome was lacking. Much later Kihara's collaborator, Matsumura (1947), found the three remaining dwarfs. These plants were the first ever produced nullisomics which became so important as instruments in investigations of the gene content of the *vulgare* chromosomes. In the offspring of some of them appeared every year a few plants of gigas habitus, discussed on p. 121.

III. Influence of Plasma upon Genome Manifestations, especially with Regard to Fertility

In the background of our statements on the fertility of the investigated species hybrids loomed the question, what role may the plasma play in the manifestation of various fertility degrees. Gradually, the relation between genome and plasma was becoming Kihara's main concern. Kihara approached the interesting problem in two series of crosses which have been since a few years in progress. 1. The object of one series was to place a genome complement in a foreign plasma. This was accomplished through successive backcrosses of the pollen parent in a cross $AA \varphi \times BB \sigma$ to the F_1 hybrid, AB (substitution backcrosses). 2. In the other series a genome complement was restored to its specific plasma. This was achieved by successive backcrosses of the female parent of a cross $AA \varphi \times BB \sigma$, as pollen furnisher, to the F_1 hybrid, AB (restoration backcrosses).

In the experiments two hybrid combinations were used which greatly differed as to the degree of relationship between the species involved. One hybrid, *Ae. longissima* $\times$ *Aucheri*, represents a combination between two species of the same group (genome S¹ and S, respectively), while the other, *Ae. caudata* $\times$ *T. vulgare*, was a hybrid between two very distantly related species of two genera.

The hybrid *Ae. longissima* $\times$ *Aucheri* has a fertility of about 6%. In the restoration series of successive backcrosses the fertility was steadily increasing, until in the fourth and fifth backcrosses the seed set was normal (about 77%) and the pollen fertility amounted to 93%. In the substitution series the fertility was also on the increase with the number of backcrosses, but remained even at its highest level much lower than in the restoration series.

The substitution backcrosses to the hybrid *Ae. caudata* $\times$ *T. vulgare* gave in many respects highly interesting results. *Ae. caudata* has black spikes, while the used *vulgare* strain was yellow. Black dominated in the F₁. In its meiosis this gene—most probably a whole block of genes—must have been transferred through crossing over to a chromosome of the *vulgare* genomes, as the *vulgare* produced in *caudata* plasma had black spikes and proved to be heterozygous in this respect. If we designate by α^c the *caudata* plasma, β the *vulgare* plasma, V the haploid ABD *vulgare* genome complement and b the gene or gene block for black, the plasma-genome formula of heterozygous *T. vulgare* in *caudata* plasma will be α^cVV^b . Moreover, without this particular gene for black spikes the *vulgare* genome complement showed a pronounced incompatibility with the *caudata* plasma. The seed set was remarkably lower in α^cVV^b than in $\alpha^cV^bV^b$. In the heterozygote the pollen α^cV was not viable, and the offspring were almost always black. Plants with yellow spikes, α^cVV , could be only obtained from crosses of α^cVV^b with normal *vulgare*, βVV , but they were so highly sterile that the strain could not be maintained.

An interesting relation between plasma and genome could be also observed in the cross between *Ae. triuncialis* and the corresponding amphidiploid, *Ae. caudata* $\times$ *umbellulata*. The fertility percentage was quite different in the reciprocal crosses in spite of the very same chromosome conjugation in both directions of the cross (Kihara and Kondo, 1943).

The first report of the coming series on genome-plasma relations is in press, as a separate publication (Kihara, 1951: Substitution of nucleus and its effects on genome manifestations).

IV. Calculation Methods Concerning the Distribution of Univalents and the Interchangeability of the Paired Chromosomes

Calculations of theoretical values of the frequency of gametes and

zygotes with various chromosome combinations in the pentaploid hybrids and their offspring led to the establishment of a few useful formulas with regard to the distribution of univalents and the eventual disclosure of interchangeable chromosomes. For convenience's sake Kihara distinguishes two types of species hybrids, namely: 1. Type AAB to which belong hybrids with at least one pair of homologous genomes and one or more single genomes. 2. Type AB which comprises hybrids containing two or more non-homologous genomes. To this type belong also haploids, obtained from diploids or allopolyploids (Kihara, 1938).

The calculations take a different form, according to which type, 1. or 2., a hybrid belongs.

1. Type AAB. A hybrid with this genome formula is the result of a cross between two species, AABB and AA. At its metaphase the chromosome configuration will be $n_{II} + n_I$ (n being the chromosome number of a genome).

The question is, what percentage of gametes with a complete A genome can be expected in this hybrid, i.e. gametes without univalents.

Let us assume that the pairing chromosomes of the two A genomes are fully interchangeable. The distribution of univalents, if it takes place at random, follows the binomial formula $(1/2 + 1/2)^n$. From this follows that the percentage of gametes with only the genome A, which would be a recombination genome (A_R), must be

$$g_i = (1/2)^n \times 100.$$

When $n=7$, as in all our cases, then $g_i = (1/2)^7 \times 100 = 0.78\%$. Should we have to consider an elimination of univalents, amounting f. inst. to 20%, the calculation would be as follows:

$$0.5 + 0.5 \times 0.2 = 0.6 \text{ and } g_i = 0.6^7 \times 100 = 2.80\%$$

How the theoretical values compare with the actual figures found in experiments can be easily examined in backcrosses of AAB to AA. The frequency of A_RA plants resulting from such crosses will correspond

Table 1. Hybrids of AAB type, in backcrosses to the AA parent. Theoretical and actual values

AAB × AA	No. of florets	No. of kernels	No. of A_RA plants	% of A_RA pl.	Theor. calc.	Univalent elimin.
1. (<i>Ae. caudata</i> × <i>cylindr.</i>) × <i>caudata</i> 7 _{II} + 7 _I Kihara, 1940	220	2	2	0.9	0.78	0.0 p=0.5
2. (<i>T. spelta</i> × <i>polon.</i>) × <i>polon.</i> 14 _{II} + 7 _I Kihara a. Wakakuwa, 1935	300	256	17	5.6	2.8-8.2	0.2-0.4 p=0.6-0.7
3. (<i>T. vulg.</i> × <i>durum</i>) × <i>durum</i> 14 _{II} + 7 _I Matsumura, 1939	167	83	18	10.8	8.2	0.4 p=0.7

to the frequency of A_R gametes (i.e. gametes without univalents) of the hybrid. We only have to divide the number of the found A_RA

plants by the number of florets among which the kernels in question occurred and to compute the percentage. The relation between the theoretical and actual figures, found on the basis of experiments, is shown in Table 1.

As Table 1 shows, the theoretical values are in good accord with those found in the backcrosses which proves that the chromosomes of the homologous (A-) genomes of the hybrids (AAB) were freely interchangeable. This was also evident from the following gene analysis.

The A_RA offspring in all three experiments of Table 1 were normal as to fertility and segregation of heterozygotic characters. Two plants, No. 1 and 2, were obtained in the first backcross of the table, (*Ae. caudata* × *cylindrica*) × *caudata*. Their genome constitution was C_RC_{caud.}. Table 2 shows the segregation ratios in the offspring with regard to a few characters.

Table 2. Mode of segregation in the offspring of C_RC_{caud.}

Plant No.	Segregating Characters	Ratio
No. 1	typica : xantha	3 : 1
No. 2	typica albino	3 : 1
Nos. 1 and 2	long awn : short awn	3 : 1
Nos. 1 and 2	(late + interm.): early	(1+2) 1
	Combination of the last two characters:	
Nos. 1 and 2	1. 1.:1. e.:s. 1.:s. e.	9 . 3 . 3 1

From the occurrence of xantha and albino seedlings in above ratios can be inferred that the C genome of *Ae. cylindrica* has these lethal characters in homozygous condition. They are counterbalanced by other genes for normal chlorophyll development in the D genome and came to light only after the conjugation of the chromosomes in question with the corresponding chromosomes of C_{caud.} which must contain the dominant alleles—otherwise *Ae. caudata* would be non-viable. On the contrary, a hypothetic diploid of the genome formula C_{cyl.} C_{cyl.} would have to be non-viable, owing to these lethal genes in homozygotic condition.

2. Type AB. To this type belong hybrids which are the result of crosses between two species with different genomes, AA and BB. Consequently, we have to assume that the number of bivalents varies between 0 and n and their partners are not interchangeable. Here we are after the percentage of gametes with a complete either A or B genome, as only such would be viable. It can be calculated (leaving crossing over out of consideration) by the formula:

$$g_2 = 1/N \times 100 \left(\sum x/2^{b+u} \right)^1$$

¹ Basic formula: $2\left(\frac{1}{2}\right)^{b+u}$ (Kihara a. Lilienfeld, 1932).

N=total number of examined PMC's, b=number of bivalents in a PMC, u=number of univalents in a PMC, x=frequency of various chromosome combinations.

Like in the foregoing case, the actual values can be found on the basis of backcrosses of AA to AB. The frequency of AA individuals will be obtained by dividing their number by the number of florets among which the corresponding kernels occurred. From the quotient the percentage can be computed. In Table 3 2 such backcrosses are listed. The calculated values are also here in accord with the figures computed on the basis of experiments. Hence the conclusion that none of the pairing chromosomes were interchangeable. Should the actual number of AA plants be significantly higher than the calculated one, we would have to assume, in accordance with the difference, that one or more chromosomes are interchangeable.

Table 3. Hybrids of AB type, in backcrosses to the AA parent. Values calculated and computed on the basis of backcrosses

AB × AA	No. of florets	No. of seeds	No. of AA plants	% of AA pl.	Calculated %	Authors
1. (<i>T. aegilopoides</i> × <i>Ae. squarrosa</i>) × <i>T. aegilop.</i> ¹	2284	2	1	0.04	0.05	Kihara a. Lilienfeld, 1935
2. <i>T. monoc.</i> 1x × 2x	a) 230	4	1	0.43	0.78	K. a. Katayama, 1933
	b) 1139	10	2	0.18	0.78	K. a. Yamashita, 1937

V. New Systematics of the Genus *Aegilops*

Genome families in the wheat-*Aegilops* group.

In the previous contributions more than once the opinion was expressed that the knowledge of genomic constitutions should be used as the basis of classification in groups of closely related species, some of them of polyploid nature. Kihara (1940) carried out such a classification for the genus *Aegilops*. This was the first attempt of such kind.

Aegilops was the subject of systematic studies of a number of taxonomists. The best known are the classifications of Eig and Zhukovsky. It is interesting to compare them with Kihara's grouping. Table 4 shows all three systems side by side. The classifications of Eig and Zhukovsky are at variance on several points, while Kihara's is almost in accord with Eig's, except for *Ae. caudata* (C genome) which was transferred to *Cylindropyrum* in full agreement with its taxonomic traits (Kihara used Zhukovsky's designations). The agreement in general of the grouping on the basis of genomes with the classification of the taxonomists shows that the *Aegilops* genomes, or rather genome families, carry characteristic phenogenetical features like the wheat genomes.

¹ Open pollination.

Table 4. Classification of the genus *Aegilops* according to

ZHUKOVSY		EIG	
<i>Amblyopyrum</i> ...	<i>Ae. mutica</i> BOISS.	7	<i>Anathera</i> <i>Ae. mutica</i> BOISS.
<i>Sitopsis</i>	<i>Ae. bicornis</i> (FORSK.)		
	JAUB. et SP.	7	<i>Platystachys</i> .. <i>Ae. bicornis</i> (FORSK.)
	<i>Ae. longissima</i> SCHW.		JAUB. et SP.
	et MUSCH.	7	<i>Ae. sharonensis</i> EIG.
	<i>Ac. speltoides</i> TAUSCH.	7	<i>Ae. longissima</i> SCHW.
	<i>Ae. Aucheri</i> BOISS.	7	et MUSCH.
			<i>Ae. speltoides</i> TAUSCH.
<i>Vertebrata</i>	<i>Ae. squarrosa</i> L.	7(14)	
<i>Polyploides</i>	<i>Ae. crassa</i> BOISS.	14, 21	<i>Pachystachys</i> .. <i>Ae. squarrosa</i> L.
	<i>Ae. turcomanica</i> ROSH.	21	<i>Ae. ventricosa</i> TAUSCH.
<i>Gastropyrum</i> ...	<i>Ae. ventricosa</i> TAUSCH.	14	<i>Ae. crassa</i> BOISS.
<i>Cylindropyrum</i> ..	<i>Ae. cylindrica</i> HOST.	14	<i>Ae. crassa</i> BOISS.
<i>Comopyrum</i>	<i>Ae. caudata</i> L.	7	<i>Ae. juvenalis</i> (THELL.)
	<i>Ae. comosa</i> SIBTH. et		EIG.
	SM.	7	<i>Monoleptathera</i> .. <i>Ae. cylindrica</i> HOST.
	<i>Ae. Heldreichii</i> HOLZM.	7	
	<i>Ae. uniaristata</i> VIS.	7	<i>Macrathera</i> .. <i>Ae. caudata</i> L.
<i>Surculosa</i>	<i>Ae. triuncialis</i> L.	14	<i>Ae. comosa</i> SIBTH. et
	<i>Ae. triunc. ssp. brachya-</i>		SM.
	<i>thera</i> BOISS.	14	<i>Ae. uniaristata</i> VIS.
	<i>Ae. triunc. ssp. Kotschy</i>		<i>Pleionathera</i> .. <i>Ae. umbellulata</i> ZHUK.
	BOISS.	14	<i>Ae. triuncialis</i> L.
			<i>Ae. variabilis</i> EIG.
<i>Polyeides</i>	<i>Ae. columnaris</i> ZHUK.	14	<i>Ae. columnaris</i> ZHUK.
	<i>Ae. biuncialis</i> VIS.	14	<i>Ae. biuncialis</i> VIS.
	<i>Ae. triaristata</i> WILLD.	14, 21	<i>Ae. ovata</i> L.
	<i>Ae. umbellulata</i> ZHUK.	7	<i>Ae. triaristata</i> WILLD.
	<i>Ae. ovata</i> L.	14	<i>Ae. triaristata</i> WILLD.

A highly interesting result of Kihara's attempt which should bring comfort to systematicists and restrain them from too subtle discussions is a simple and obvious demonstration of the cause of their scruples and doubts which they so often experience¹, when attempting to subdivide plant groups which contain polyploids. In order to explain it, let us look first at the genome families participating in the make-up of the genus and their distribution:

1. Cⁿ family (Cⁿ stands for various small modifications of a genome which is related to the C genome), with Cⁿ of *Ae. umbellulata* and its various modifications, characterizes the *Polyeides* division.

2. C family of the *Cylindropyrum* division. The C of *cylindrica* is truly homologous with the C of *caudata*.

3. M family, with numerous modifications. Two are represented in

¹ I speak from my own experience—obtained from systematical studies of *Hepaticae* and, also, when I was preparing the systematics of *Potamogetonaceae* and a few other groups for the Flora of Poland.

ZHUKOVSKY, EIG and KIHARA

KIHARA		
<i>Polyeides</i>	<i>Ae. umbellulata</i> ZHUK.	C ^u
	<i>Ae. ovata</i> L.	C ^u M ^o
	<i>Ae. triaristata</i> WILLD. 4x	C ^u M ^t
	<i>Ae. triaristata</i> WILLD. 6x	C ^u M ^t +(?)
	<i>Ae. columnaris</i> ZHUK.	C ^u M ^c
	<i>Ae. biuncialis</i> VIS.	C ^u M ^b
	<i>Ae. variabilis</i> EIG.	C ^u S ^v
	(incl. <i>Ac. Kotschyi</i> BOISS.)	
	<i>Ae. triuncialis</i> L. (incl. <i>Ae. persica</i> BOISS.)	C ^u C
<i>Cylindropyrum</i>	<i>Ae. cylindrica</i> HOST.	CD
	<i>Ae. caudata</i> L.	C
<i>Comopyrum</i>	<i>Ae. comosa</i> SIBTH. et SM.	M
	(incl. <i>Ae. Heldreichii</i> HOLZM.)	
	<i>Ae. uniaristata</i> VIS.	M ^u
<i>Amblyopyrum</i>	<i>Ae. mutica</i> BOISS.	Mt
<i>Sitopsis</i>	<i>Ae. speltoides</i> TAUSCH.	S
	(incl. <i>Ae. Aucheri</i> BOISS.)	
	<i>Ae. longissima</i> SCHW. et MUSCH.	S ^t
	(incl. <i>Ae. sharonensis</i> EIG)	
	<i>Ae. bicornis</i> (FORSK.) JAUB. et SP.	S ^b
<i>Vertebrata</i>	<i>Ae. squarrosa</i> L.	D
	<i>Ae. crassa</i> BOISS. 4x	DJ
	<i>Ae. crassa</i> BOISS. 6x	DJ+(?)
	<i>Ae. ventricosa</i> TAUSCH.	DM ^v

the *Comopyrum*-, one in the *Amblyopyrum*-, five in the *Polyeides*- and one in the *Vertebrata*- division. The M family is, as we see, scattered over most of the divisions. Correspondingly, its members show a wide range of variation as to the degree of their interrelations.

4. D family, represented in two divisions, with *Ae. cylindrica* in *Cylindropyrum* and *squarrosa*, *ventricosa* and *crassa* in *Vertebrata*. The D's of the first three are truly homologous, while the *crassa* D is on a slightly farther plane.

5. S family, with three modifications in *Sitopsis* and one in *Polyeides*.

6. The still little known J family of the two *crassae*, with no representative elsewhere. From the morphological point of view J seems to be nearly related to M.

If we add the wheat genomes:

7. A family, common to all four groups.

8. B family, represented in the three well known groups.

9. G family of the *Timopheevi* group.

(The Dinkel genome D belongs to family 4.)

Families 7, 8 and 9 have no representatives in the *Aegilops* group.

The above survey shows the scattering of the *Aegilops* genomes—some more, other less—over various divisions¹. This is the cause of the difficulties encountered by plant taxonomists. If we draw connecting lines between the genomes belonging to the same families, as it is done in Table 5 (Kihara, 1947), we have a demonstration *ad oculos* of the reticulate character of the interspecific relations. In consequence, it is evident that it may be a matter of personal taste, how a systematicist will place a polyploid species which partly shares its genomes with species of two or more divisions (comp. Stebbins, 1947).

Table 5. Genome affinities in the *Triticum-Aegilops* group

It shall be mentioned in this connection that an attempt to classify our group on karyomorphological basis was made by Senjaninova-Korezagina (1932). The result is almost in full accord with Kihara's system.

¹ Informations as to—and proofs of—the statements concerning intergenomic relations can be looked up in contributions VII (1939) and IX (1949).

But it should not be overlooked that karyomorphological investigations are very difficult, especially in our group. Further, karyophenotypes are known in general to be very variable (Yamamoto, 1938). The unreliability of the method is proved by Senjaninova-Korczagina's analysis of *Ae. cylindrica* which according to her should have a *bicornis* genome. Or her finding that *Ae. persica*, a variety of *Ae. triuncialis*, should be on the grounds of a divergent karyotype transferred as a separate species to another section (from *Polyeides* to *Cylindropyrum*).

Not without interest is the geographical distribution of the nine diploid species subdivided by Kihara (p. 103) in three groups. As Table 6 and Fig. 1 show, the habitats of the three genome families, C, M

Fig. 1. Geographical distribution of the diploid analysers.

and S, make it appear quite possible that the members of each of the groups¹ were derived from a common ancestor. Only *Ae. squarrosa* seems to be out of place in the second group. Either its original habitat had undergone long ago changes, or the available pertaining data are incorrect and require a revision. The same table also shows that the genomes C and M had ample opportunity to mix and to produce the allopolyploid species of *Polyeides*, the most diversified division of the genus (Table 4). The possibility of entering into hybrid combinations was for the third group (S family) more limited. As usual in such cases, almost all polyploid species of the *Polyeides* division are spread over a much larger area than the diploids with the genomes C or M. *Ae. ovata* and *triaristata* occupy almost the whole area of the genus. The only exception represents *Ae. columnaris* which occupies according to the data on hand a very restricted area.

¹ Mⁿ seems to have an isolated habitat, but it occurs sporadically in the overlapping areas of the other members of the M family (Table 6).

VI. Autopolyploidy and Allopolyploidy

The genomes of an autopolyploid are homologous, i. e. the linear arrangement of the loci in the pairing chromosomes is identical. In contradistinction to an allotetraploid, AABB, (comp. p. 103), an autotetraploid, AAAA, will produce in a cross with the corresponding analyser AA either trivalents or $x_{II} + x_I$ (x =number of chromosomes in one genome), and only the latter configuration in crosses with all other analysers. Artificial autopolyploids have been many times produced in experiments. The question, if autopolyploids of reliably known origin occur in nature, was fully discussed by Stebbins (1947). From the above definition follows that polyploids obtained from intraspecific fertile crosses may be considered as autopolyploids. The homologous chromosomes of autopolyploids may conjugate in pairs, like in *Fragaria* (Lilienfeld, 1936), or they may form polyvalents. In the first case the genomically conditioned fertility will be good, in the second the distribution of the polyvalent chromosomes is apt to cause partial sterility.

Table 6. Distribution of the nine diploid analysers

Group	Analyser	Genome	Distribution
C	<i>Ae. caudata</i>	C	Southern part of Balkan Peninsula, Crete, Asia Minor, Syria, Assyria, Northern Mesopotamia.
	<i>Ae. umbellulata</i>	C ⁿ	Syria, Mesopotamia, Persia, Asia Minor.
M	<i>Ae. comosa</i>	M	South & South-Western Balkan Peninsula, Western Asia.
	<i>Ae. uniaristata</i>	M ⁿ	North-Western Balkan Peninsula, Morea, Asia Minor, Scutari, Maltepe.
	<i>Ae. squarrosa</i>	D	Kashmir, Afghanistan, U.S.S.R. Central Asia, Persia, Transcaucasia.
	<i>Ae. mutica</i>	Mt	Turkish Armenia, Asia Minor, Paphlagonia, Cappadocia, Lydia.
S	<i>Ae. speltoides</i>	S	Asia Minor, Northern Mesopotamia, Syria, Palestine.
	<i>Ae. longissima</i>	S ^l	Palestine, Egypt.
	<i>Ae. bicornis</i>	S ^b	Southern Palestine, Lower part of Egypt, Cyrenaica, Sinai Peninsula.

In a true allopolyploid the non-homologous genomes are supposed to have lost all affinities, and pairing ought not to occur between them (Schema 1 and p. 104).

Our experiences won from an unusually large material of interspecific crosses show that strict non-homology, as defined above, does not occur in our group. This is probably also the case with other groups of intercrossable species. All non-homologous genomes of the

Triticum-Aegilops group showed segmental similarities, at least in one part of their chromosomes, in the absence of their homologues. In the presence of the homologous genomes semihomologous pairing was suppressed; from this the prevalence of preference pairing in our group may be inferred. The segmental similarities showed a wide range as to their amount and the number of chromosomes involved. Genomes C and S f. inst. showed the weakest genomatic relations, while the *triuncialis* genomes C and Cⁿ showed quite a deal of segmental similarities (manifested in crosses with rye, Kihara, 1937, and other crosses) which suggested that *Ae. triuncialis* is like *Primula Kewensis* not far from being an autotetraploid. Owing to the lack of pronounced preferential pairing in the latter, its cytological and genetical behavior appears to be quite different, since it shows a strong admixture of autopolyploidy.

Stebbins (1947) emphasizes the need of further classification of allopolyploids, in order to give a special name to those of mixed nature, like *Primula Kewensis* a. o. He proposes the term "segmental allopolyploidy". I do not believe that it is quite suitable, as it implies, by logical inference, that only the segmental allopolyploids are characterized by segmental similarities. In reality all polyploids derived from species crosses are in this sense, potentially or actually, segmental polyploids. The differences are only of quantitative nature, and the manifestation depends on the amount of segmental similarities and absence or presence of preferential pairing. Therefore, I should prefer other terms, f. inst. isosyndetical and iso- + anisosyndetical allopolyploids¹. In the first case, in the allotetraploid AABB genome A would always pair with A and B with B. In case of iso- + anisosyndesis A may pair also with B. The observed iso- + anisosyndetical polyploids show a vast range of variation as to the amount of iso- and anisosyndesis. The complexity and variety of phenomena related to polyploidy are so great that sometimes attempts at typifying them seem of elusive value.

VI. Cytological Investigations

The main result of these investigations was the clearing up of the succession of meiotic stages subject—at that time—to many controversial reports. Also, it was proved beyond doubt that unreduced sporocytes, which give rise to allopolyploids in nature, occur frequently in our group, as the result of breaking down of regular meiotic processes. The stage of occurrence of the phenomenon was shown to be in most cases the early anaphase of the first maturation division. From the fusion of two unreduced gametes of the hybrid ABD (*T. dicoccoides* × *Ae. squarrosa*) Kihara obtained his artificially synthesized *T. spelta* (1948 and 1949). In

¹ I realize the defects of this terminology; its only merit is that it is not misleading.

similar manner an amphidiploid resembling very nearly *T. vulgare* was synthesized from a cross between *T. persicum* and *Ae. squarrosa* (Kihara et alii, 1950).

VII. Segmental Differentiation of Genomes

From the numerous intergenomational segmental (semihomologous) relations it was inferred that the structural differentiation of genomes was brought about through segmental changes, like reciprocal translocations and inversions accompanied by other structural changes, f. inst. duplications or deficiencies. Owing to the hence resulting sterility in backcrosses the isolated genomes continued to change in similar way step by step and move apart. In the long run the structural differentiation became more and more pronounced, but the estrangement of genomes in our group did never go so far as to eliminate all segmental (semihomologous) relations.

Segmental changes are a frequent phenomenon in species hybrids, induced through the bringing together of more or less nonhomologous genomes. The new surroundings, created in the foreign plasma for the genome (or genomes) of one of the parents may take part in it (Kihara and Kondo, 1943). As to the role of structural genome differentiation in evolution, it must be left out of consideration in this short report on the main results of our experiments. We also refrain from discussing, in addition to structural changes, many other differentiation possibilities which should be considered, if an entire picture of genome development had to be unfolded. We will return to these subjects in the future.

In 1932 (contribution IV) we expressed the opinion that either in a natural way or caused by X-Rays a vast variety of segmental changes may be effected also in intraspecific crosses and pure species as well (in the latter mostly through treatment with X-Rays). In this connection we mentioned that it would be even possible, but not probable, that f. inst. such reciprocal translocations could occur as to repeat the case of *Oenothera*. This prediction—so cautiously expressed—came true. As a result of ten year studies Dr. K. Yamashita, a member of Kihara's institute, obtained in the Einkorn group, after X-Ray treatments, strains which imitate the *Oenothera* case in all particulars except for the mechanism of balanced lethals (1950 a and 1950 b).

Another interesting case, where the obvious explanation seemed scarcely probable, represents our experience with the hybrid *T. aegilopoides* × *Ae. squarrosa* (1934). On the grounds of its behavior it seemed that one chromosome of the A genome is interchangeable with one of the D genome. Considering the hitherto known relations between the two genomes, this did not seem very probable. Several years later Sears (1939) found that the lack of one chromosome pair of the genome D can

be compensated by the duplication of one A pair. This makes our finding comprehensible.

In this connection should be mentioned a highly interesting case which parallels the aforesaid finding of Sears. Among the dwarflike nullisomics of Kihara (Kihara a. Wakakuwa, 1930) especially in the e-line, appear every year a few plants of remarkably vigorous growth, also taller than the parental species. The investigation of the first metaphase showed regularly the configuration $19_{II}+1_{IV}^1$. Evidently the lack of one D-pair is counterbalanced in such a striking manner by the duplication of one A- or B-pair, which may contain growth controlling genes. Such 42 chromosome plants could be of great practical importance (Kihara and Wakakuwa, 1930 and Kihara and Matsumura, 1942).

Conclusion

The knowledge of genomic relations, especially in a group in which polyploidy occurs, opens new vistas to the systematicist and geneticist as well as to the plant breeder. It will allow a deeper insight into the nature of the material treated by the systematicist and enable him to establish rational working methods. To the geneticist it will always provide an inexhaustible source of new findings. It may, also, through reconstruction of existing allopolyploid species be of help in questions of phylogeny.

The same can be said of the importance of polyploidy to the plant breeder. Production of autopolyploids has become since the discovery of colchicine effects an important instrument in plant breeding. Accepted on a broad basis in Svalof, it already produced there excellent results. In Japan it was introduced to plant breeding by Kihara. His last contribution is a triploid sugar beet (Mochizuki and Matsumura, 1950) with 10-12% higher sugar content than in the diploid.

In the long range, experimental operating with genomes and genome abnormalities may even bring much greater improvements. It is quite conceivable that new, greatly improved amphidiploids will be synthesized. Also, the thorough knowledge of the gene content of single *vulgare* chromosomes, which has been made possible owing to Sears' nullisomics², will make it possible to replace the unwanted genes with others through transfers from one genome to another— a method already practiced.

In the course of such considerations one becomes inclined to think that it would be of great use to mankind to assemble in a center like Beltsville, United States, a collection of living genomes, genome combi-

¹ The first gigas plants found by Kihara had 41 chromosomes. In their offspring appeared 42 chromosome plants.

² Sears identified 19 nullisomics; the missing two provided Kihara's institute (Kihara and his co-workers found all seven D-chromosomes nullisomics).

nations and such helpful abnormalities like the nullisomics. They could be distributed to research places of other countries according to their needs.

REFERENCES

- Aase, H. C., 1930. Cytology of *Triticum*, *Secale*, and *Aegilops* hybrids with reference to phylogeny. Res. St. State Coll. Wash.
- Dobzhansky, T., 1941. Genetics and the origin of species.
- Eig, A., 1929. Monographisch-kritische Übersicht der Gattung *Aegilops*. FEDDE Repert. Spec. nov. 55.
- Kihara, H., 1919. Über zytologische Studien bei einigen Getreidearten. Bot. Mag. Tokyo, 33.
- 1924. Cytologische und genetische Studien bei wichtigen Getreidearten. Mem. Coll. Sci. Kyoto Univ. B., 1.
- 1925. Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. I. Jap. Journ. Bot., 2.
- 1929. Conjugation of homologous chromosomes in genus hybrids *Triticum* × *Aegilops* and species hybrids of *Aegilops*. Cytologia, 1.
- 1930. Genomanalyse bei *Triticum* und *Aegilops*. II. Cytologia, 2.
- 1932. Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. II. Jap. Jour. Bot., 6.
- 1937. Genomanalyse bei *Triticum* und *Aegilops*. VII. Mem. Coll. Agr. Kyoto Univ., 41.
- 1938. Cytogenetics of species hybrids. Current Science. Special number on "Genetics" March, 1938.
- 1940. Verwandtschaft der *Aegilops*-Arten im Lichte der Genomanalyse. Der Züchter, 12.
- 1944. Die Entdeckung des DD-Analysators beim Weizen. Agriculture and Horticulture, Tokyo, 19.
- 1947. The genus *Aegilops* classified on the basis of genome analysis. In Jap. Seiken Ziho, 3.
- 1949. Genomanalyse bei *Triticum* und *Aegilops*. IX. Cytologia, 14.
- et alii, 1950. Morphology and fertility of five new synthesized hexaploid wheats. Seiken Ziho, 4.
- u. Y. Katayama, 1931. Genomanalyse bei *Triticum* und *Aegilops*. III. Cytologia, 2.
- a. N. Kondo, 1943. Studies in amphidiploids of *Aegilops caudata* × *Aegilops umbellulata* induced by colchicine. Seiken Ziho, 2.
- u. F. A. Lilienfeld, 1932. Genomanalyse bei *Triticum* und *Aegilops*. IV. Cytologia, 3.
- u. — 1934. Genomanalyse bei *Triticum* und *Aegilops*. VI. Cytologia, 6.
- a. — 1948. Chromosome pairing and fertility in a new synthetic *Triticum spelta*. Ac. Pol. Sci. Let. Krakow.
- a. — 1949. A new synthesized 6x-wheat. Proc. VII. Int. Congr. Gen.
- u. S. Matsumura, 1940. Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. XII. Jap. Jour. Bot., 11.
- u. — 1941. Genomanalyse bei *Triticum* und *Aegilops*. VIII. Cytologia, 11.
- u. — 1942. Über die Univalentenelimination in den verschiedenchromosomigen Nachkommen des pentaploiden *Triticum*-Bastards. Jap. Journ. Bot., 12.
- u. I. Nishiyama, 1930. Genomanalyse bei *Triticum* und *Aegilops*. I. Cytologia, 1.
- a. — 1930. Dwarf plants with 40 chromosomes in the progeny a pentaploid *Triticum* hybrid. Jap. Journ. Gen., 5.
- u. Wakakuwa, 1935. Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. IV. Jap. Jour. Bot., 7.
- — u. Y. Yamamoto, 1933. Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. III. Ibidem. 6.
- u. I. Yamada, 1942. Ein Fall von Plasmonwirkung auf das artfremde Genom. Seiken Ziho, 1.
- Kondo, N., 1941. Chromosome doubling in *Secale*, *Haynaldia*, and *Aegilops* by colchicine treatment. Jap. Journ. Gen., 17.
- Lilienfeld, F., 1936. Karyologische und genetische Studien an *Fragaria*. II. Jap. Journ. Bot., 8.

- Lilienfeld, F., a. H. Kihara, 1934. Genomanalyse bei *Triticum* und *Aegilops*. V. Cytologia, 6.
- Matsumoto, K. a. N. Kondo, 1942. Two new amphidiploids in *Aegilops*. Jap. Journ. Gen., 18.
- Matsumura, S., 1936-1940. Untersuchungen über die pentaploiden *Triticum*-Bastarde. V-XI. Jap. Jour. Boty 8-11.
- 1947. Chromosomenanalyse des Dinkelgenoms auf Grund zytogenetischer Untersuchungen an pentaploiden Weizenbastarden. La Kromosomo, 3-4.
- McFadden, E. S. a. E. R. Sears, 1944. The artificial synthesis of *T. spelta*. Rec. Gen. Sci. Am.
- Mochizuki, A. a. S. Matsumura, 1950. Genetic and cytological studies on the genus *Beta*. IV. Seiken Ziho, 4.
- Sakamura, T., 1918. Kurze Mitteilung über die Chromosomenzahlen und die Verwandtschaftsverhältnisse der *Triticum*-Arten. Bot. Mag. Tokyo, 32.
- Sax, K., 1918. The behavior of chromosomes in fertilization. Genetics, 3.
- Sax, K. a. H. J. Sax, 1924. Chromosome behavior in a genus cross. Genetics, 9.
- Sears, E. R., 1944. Cytogenetic studies with polyploid species of wheat. Genetics, 29.
- 1941. Amphidiploids in the 7-chromosome *Triticinae*. Univ. Mo. Coll. Agr.
- 1948. The cytology and genetics of the wheats and their relatives. Advances in Genetics. II.
- Senjaninova-Korczagina, M., 1932. Karyo-systematical investigations of the genus *Aegilops*. Bull. Appl. Bot. Gen. and Pl. Breed. Ser. 2.
- Stebbins, G. L., 1947. Types of polyploids: their classification and significance. Advances in Genetics. I.
- Zhukovsky, P. M., 1928. A critical-systematical survey of the species of the genus *Aegilops* L. Bull. Appl. Bot., 18.
- Yamamoto, Y., 1938. Karyogenetische Untersuchungen bei der Gattung *Rumex*. VI. Mem. Coll. Agric. Kyoto Univ., 43.
- Yamashita, K., 1950 a. Studies on X-ray induced reciprocal translocations in Einkorn wheat. I. Analysis of some new RT types. Seiken Ziho, 4.
- 1950 b. A synthetic complex heterozygote in einkorn wheats: *aegilopoides* · *monococcum*. Proc. Jap. Acad., 26.