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Cytogenetics and Cereal Breeding

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The author's aim on writing the present article is to outline and reunite some facts and investigations made latterly in the field of Cytogenetics which are the basis for the development of new breeding techniques and methods. Cereal species are those to which research workers' special attention has been paid. This review will only concern these species.

As indicated above, it is not intended to make an exhaustive review of the topic but to put together and diffuse the enormous applications and wide horizons which have been open to cereal breeders.

Contribution of Cytology to Plant Breeding was exiguous until a few years ago. Undoubtedly some cytogenetic basic knowledge was applied to plant breeding, but such knowledge was the lesser part. Cytogeneticists and plant breeders did not coordinate their efforts; perhaps, occasionally, the cytogeneticist tried to study, analyze and explain with the microscope that material which was interesting for the plant breeder.

On the contrary, it seldom happened that plant breeders might use in their experiences the material which showed special interest for the cytogeneticists.

As stated by CAMARA (1960), in the last years Plant Breeding is looking for new effective and fast methods which permit the obtention of new varieties in a more conscious way. In our opinion these methods are those based on the application of Cytogenetics.

The lines of work which are possible in a cytogenetic programme of Cereal Breeding can be summarized as follows:

1. Changes in plody level
    - a) Polyploidy (fertility and aneupolyploidy).
    - b) Haploidy.
2. Chromosome aberrations
    - a) Structural changes (translocations, duplications, etc.).
    - b) Changes in number of chromosomes (aneuploidy).
3. Introduction of alien variation
    - a) Hybrids and their amphiploids
    - b) Chromosome addition lines
    - c) Chromosome substitution lines
    - d) Gene transfer
    - e) Gene recombination (genetic control of meiotic pairing: Chromosome V (5B)).
4. Intervarietal substitution.
5. Genome extraction and construction.

References of authors and papers made in this review will not be excessively wide or exhaustive, but one will try that they be the most representative of the progress made in the application of Cytogenetics to Cereal Breeding. Wheat, barley, oats and rye will be the species concerned.

1. CHANGES IN PLOIDY LEVEL

a) *Polyploidy* (Fertility and aneuploidy).

The use of artificial polyploidy as a tool of Plant Breeding assesses an important step in the development of this Science. Almost all cultivated species have been tested in relation to autotetraploidy with the most diverse results.

Among the grain crops cultivated by man, as in the case of cereals, only the rye autotetraploid forms have been used as a crop in extensive culture because they can compete in quality and yield with the original diploids (MÜNTZING, 1951). The German variety «Petkus», the Swedish «Stal» and the Spanish «Gigantón» (TJIO, SÁNCHEZ-MONGE y ALVAREZ PEÑA, 1953) —this last obtained at the Estación Experimental de Aula Dei— are good examples.

As a rule, the visible phenotypic effects produced by chromosome doubling are conspicuous in every species: greater vigour, wider and darker leaves, bigger fruits and seeds, and so on. However, seed setting is not good, this being the fact for which autotetraploid forms —except in rye— are not of economical value.

The low percentage of seed set and bad formation of endosperm are partially due to meiotic irregularities. The occurrence of meiotic multivalents and their unequal anaphasic distribution brings about aneudiploid gametes and, as a consequence of the fusion of these gametes, aborted and shrivelled seeds are formed.

With these facts in mind, it was thought that the selection of *foundation plants* after their meiotic behaviour might be of value for breeding purposes, assuming that meiotic regularity and fertility must be related (PLARRE, 1954; BREMER and BREMER-REINDERS, 1954; HILPERT, 1957, etc.).

In order to avoid the formation of meiotic multivalents, CALDECOTT (1961) indicates the possibility of obtaining by radiation «pseudoautopolyploids» in which there were not multivalent associations.

When the tetraploid varietal population of rye has been established, it is necessary to maintain its level of ploidy diminishing the percentage of aneuploid individuals in such populations. HAGBERG and ELLERSTRÖM (1959) studied the theoretical and practical aspects of the problem.

Thus far not any autotetraploid form of wheat, barley or oats showed having practical application in Agriculture. This agrees with the general criterion that only allogamous species with a low number of chromosomes are appropiate to bred by means of induced polyploidy. Rye is an allogamous species with $2n = 14$ chromosomes.

Shebeski has attempted to obtain by radiation autotetraploid forms of barley of value for Agriculture (UNRAU and MCGINNIS, 1958). Perhaps his aim was to make up the «pseudoautotetraploids» to which CALDECOTT (1961) referred.

b) *Haploidy.*

NEI (1963) discussed the advantages of using the *haploid method* in Plant Breeding in order to obtain pure lines from heterozygous populations both in autogamous and allogamous plants.

The high frequency of haploids (eu— and aneuhaploids) found in the offspring of mono-I individuals of the wheat variety *Holdfast* induced RILEY (1965) to consider the possibilities of applying a new and very valuable cytogenetic method to Wheat Breeding. If it should be possible to induce haploidy in F_1 generation of intervarietal crosses, the first products of segregation and recombination might be isolated. Latter chromosome doubling should bring about new homozigous diploid varieties, thus avoiding the segregant generations in the programme of obtention of new varieties.

2. CHROMOSOME ABERRATIONS

a) *Structural changes.*

Aberrations produced by changes in the chromosome structure —such as inversions, translocations, duplications and deletions— can be easily induced by physical or chemical agents as a consequence of a breakage-fusion mechanism. All these aberrations are of interest as to Plant Breeding.

Of the four cereals with which this article is concerned, barley is the most investigated species as to structural chromosome changes. For example, as many as 136 translocations have been identified and analyzed in the variety *Bonus* (HAGBERG, 1962). In addition to the importance of these changes in barley breeding as possible sources of variation, translocations may be the origin for ulterior obtention of duplications and deletions as a result of structural rearrangements produced in crosses between individuals having translocations involving the same chromosomes. If the material is well known cytologically, it is possible to select those chromosome segments carrying favourable genes in order to obtain translocations and duplications whose phenotypic effects might be of interest in Agriculture.

Heterosis or hybrid vigour has a great importance in Breeding and continuous efforts are being made to exploit it to commercial level.

Works carried out to produce hybrid seed in maize, sorghum, onion, etc., are good examples. In all these cases special techniques are required to obtain and maintain the pure lines.

Fixation of heterosis as a true bred condition would be of the greatest practical value. Since diploid individuals *Vv* of barley yield more than those with *VV* or *vv* genotypes, it is logical to think of individuals *VVvv*, obtained by a duplication of the chromosome segment carrying such genes, also showing heterosis. With these facts in mind, BEAR (1960; cited by BURNHAM, 1962) radiated heterozygote diploid plants of barley in order to obtain heterotic individuals *VVvv*.

The spontaneous occurrence in Nature of the *structural hybrids*, such as those found in *Oenothera* sp., *Rhoeo dislocor* (DARLINGTON, 1929), *Hypericum punctatum* (HOAR, 1931), *Paeonia californica* (STEBBINS and ELLERTON, 1939), etc. (all of them cited by BURNHAM, 1962), induce one to think of the possibility of obtaining artificial permanent hybrids in species of agronomic interest. The perspective to maintain the heterozygosis in autogamous plants as a true bred condition is of the most importance. YAMASHITA (1951) was able to synthesize a series of structural hybrids in *Triticum monococcum* ($2n = 14$), obtaining all the meiotic configurations ranging from one four-chromosome ring plus five bivalents to one fourteen-chromosome ring. NISHIMURA and collaborators have investigated the formation of metaphasic rings in barley. TULEEN (1965) obtained by X-radiation plants of barley with a 14-chromosome ring.

The possibility of suppressing genes with deleterious effects by means of deletions may be another application of Cytogenetics to Plant Breeding; as well as the utilization of telocentrics in certain breeding cytogenetic techniques for replacing nullisomics in order to overcome problems of vigour and fertility.

BURNHAM (1962) studied in detail the theory of chromosome structural changes and their application to Plant Breeding. KUCKUCK (1958) and CAMARA (1960), among others, have pointed out the utilization of translocations in Plant Breeding.

b) *Changes in the number of chromosomes* (*Aneuploidy*).

Studies on aneuploidy have a great importance both from a theoretical and practical point of view. Detailed studies of this subject depart from the limits of this review. Therefore, the most important steps concerning the development of the aneuploidy investigations in cereals will be only pointed out herein.

Occurrence of aneuploidy in wheat and oats is more frequent than in barley and rye because the former species are allopolyploids and the second ones are diploids. The loss of some chromosome of the normal complement has lethal effects in diploid individuals because the genetic material is not replicated. So far, only hyperploid individuals of trisomic or tetrasomic types have been found in barley and rye.

The only two references on trisomy in rye goes back many years (TAKAGI, 1935; MÜNTZING and PRAKKEN, 1941) and not any rye trisomics or tetrasomics have been reported from that date.

Barley trisomics have been investigated extensively and the complete series of primary trisomics were established by TSUCHIYA (1954) and RAMAGE (1954, cited by TSUCHIYA, 1960) in *Hordeum spontaneum* C. KOCH var. *transcaspicum* Vav. and in *Hordeum vulgare* L. variety *Mars*, respectively. Thereafter, TSUCHIYA (1964) established also the complete trisomic series in a two-rowed cultivated variety.

The theorical importance and utility of the trisomic series is inferred by the possibility to relate chromosomes to linkage-groups, thus giving very valuable genetic information for further breeding works.

Tetrasomics in barley are very rare. This kind of aneuploids were reported for the first time by TSUCHIYA (1962).

By contrast with the diploid species, individuals of allopolyploid species are able to survive the loss of some chromosome because they have replicated their genetic material. Hypopolyploids (monosomics and nullisomics) in addition to hyperpolyploids (tri— and tetrasomics) are possible both in wheat and oats.

WINGE (1924) was the first who reported the ocurrence of monosomics in wheat on studying certain speltoid types. Since then, investigations on wheat aneuploidy were increased until they reached their climax in Sears' works. His publication of 1954 may be considered as the «trigger» of the studies concerning wheat aneuploidy (SEARS, 1954).

Sears obtained the complete monosomic series in the variety *Chinese Spring* utilizing haploids and nulli-III as chief sources of aneuploidy (SEARS, 1939a, 1944). This monosomic series has been utilized by investigators all over the world. Complete monosomic series have been established at the present in many other commercial varieties, such as *Rescue* and *Cadet* (LARSON), *Redman* and *Prelude* (PETERSON and CAMPBELL), *Thatcher* and *Lemhi* (KUSPIRA), *Kharkov* (JENKINS), *Wichita* (HEYNE), *Koga* II and *Capelle-Desprez* (RILEY and collaborators), among others.

The importance of aneuploidy in theoretical studies of genetics is enormous, but here will only be considered its practical value for Agriculture as cognation of three different fields of Cereal Research: Genetics, Cytogenetics and Breeding.

The lack of vigour and fertility in nullisomics and the chromosome instability of monosomics, trisomics and tetrasomics are obstacles which can be hardly overcome in order to utilize wheat aneuploid varietal populations as commercial varieties. It can be possible that nulli-tetrasomic combinations overcome the above problems.

In regard to varietal purity, RILEY and KIMBER (1961) pointed out the importance of cytogenetic structure in varietal populations of wheat. Their conclusions are interesting for those official organisms which must keep up the purity of commercial varieties. The author has analyzed the same problem in a standard Spanish variety (LACADENA, unpublished).

Practical applications of aneuploid, such as chromosome addition and substitution lines, will be discussed later.

Species of the genus *Avena* can be classified in three categories —diploids, tetraploids and hexaploids— according to the chromosome number.

It is known that the hexaploid species *A. sativa* and *A. byzantina* are the most important among the cultivated oats. The acreage sowed with *A. sativa* surpasses 80 % of the total. Other species —*A. strigosa* (diploid), *A. Abyssinica* (tetraploid), *A. nuda* (hexaploid)— are also cultivated but in much lesser extension (COFFMAN, 1961). All the varieties cultivated in Spain belong to *A. sativa* and *A. byzantina* species and possibly in excess of 90 % of the acreage corresponds to *A. sativa* (VILLENA, personal communication).

The philogenetic relationships among species of genus *Avena* are not so clear than those of *Triticum*. According to RAJHATHY and MORRISON (1959), *Avena sativa* is an allohexaploid with genomes A, C and D; therefore the occurrence of aneuploid individuals in oat populations is possible.

In spite of the fact that almost 40 years ago HUSKINS (1927) reported for first time the *fatuoid* monosomic, studies on oat aneuploidy were not intensified until the last few years (COSTA-RODRIGUES, 1954; RILEY and KIMBER, 1961; MCGINNIS, 1962; HACKER and RILEY, 1963). We do not doubt these works are the prelude to the development of oat aneuploidy investigations which will lead to the applications of Cytogenetics to Oat Breeding.

Riley and Kimber (1961), McGinnis (1962) and Hacker and Riley (1963) found in varietal populations of oats such percentages of spontaneous aneuploidy which raise the same problem as the wheat populations do.

3. INTRODUCTION OF ALIEN VARIATION

For many years plant breeders have intented to incorporate favourable characters —such as resistance to diseases and drought, etc.— from wild speces into cultivated plants.

Winge is said to be the first investigator who recognized the importance of interspecific crosses as a tool of Plant Breeding.

a) *Hybrids and their amphiploids.*

In order to gather in only one individual the favourable characters from different species, interspecific hybrids —or even intergeneric ones in some cases— have been obtained in the four cereal species (wheat, barley, oats and rye) which this review deals with. So, resistances to rust, drought and shattering, tillering ability, etc., were intended to be incorporated to wheat by means of the *Triticum* sp. × *Aegilops* sp. hybrids. With *Triticum* sp. × *Agropyron* sp. hybrids, frost and drought resistance, saline soil adaptability and perennial condition of *Agropyron* species were tried to be added to wheat. Sando (1935) reported the occurrence of intergeneric hybrids between *Triticum* sp. and *Haynaldia villosa*.

Cultivated barley has been crossed with other species of genus *Hordeum* such as *spontaneum, agriocrithon, jubatum, bulbosum* and *nodosum*. Intergeneric hybrids were obtained with *Elymus arenarius* and *Elymus giganteus*.

Crosses between *Secale cereale* and *Secale montanum* have been made in order to transfer the perennial condition from *S. montanum* to cultivated rye.

All these data —cited by SÁNCHEZ-MONGE (1955)— and other similar ones show the efforts made by plant breeders to incorporate to cultivated species the valuable characters of related wild species.

Interspecific and intergeneric hybrids are sterile by their own nature and this sterility led to obtain fertile amphiploids. Artificial induction of amphiploidy was greatly facilitated after colchicine was discovered as a polyploidizing agent. EIGSTI and DUSTIN (1955) extensively reviewed the topic.

In cereals, the obtention of *Triticale* (MÜNTZING, 1939, 1955, 1956; O'MARA, 1948, 1953; SÁNCHEZ-MONGE, 1956, 1958a; PISSAREV, 1956) by chromosome doubling of the *Triticum* sp. × *Secale cereale* hybrids meant a positive advance in Wheat Breeding. It was intended to reunite in this new cereal the milling and baking quality of wheat with the ability of rye to grow on poor and dry soils.

Immediate application of triticale as a new cultivated cereal species in Agriculture is limited by two main obstacles: low fertility —measured in per cent of seed setting— and the bad formation of the endosperm at the last steps of seed maturity, resulting in a decrease of milling quality as a consequence of increasing the seminal cover proportion.

Triticale fertility may be related with that of the rye parent; for which it could be profitable to utilize self-fertile inbred lines as rye genitor. SÁNCHEZ-MONGE (1958a) obtained by this way triticale plants with 80-90 % of fertility. Except the *Triticale* type *dicoccoides* which show certain tendency to allogamy, all of the hexaploid *Triticale* obtained by SÁNCHEZ-MONGE are autogamous. For that, undoubtedly, the rye genome acting under an autogamous condition, phenomenons of gene self-incompatibility will have to become apparent. This gene self-incompatibility —and not the wheat-rye genome interaction— is responsible for the low fertility.

The bad formation of the endosperm may be attributed to the unbalanced nucleus-cytoplasmic interaction in the 3n cells. This unstable equilibrium is greater in octoploid than in hexaploid triticales.

It is possible that Triticale Breeding overcomes the above difficulties and this new cereal might compete in yield and quality with wheat in marginal areas of this cereal. Results of the first trials for production and quality made in Canada have been highly satisfactory (SHEBESKI, 1962).

Although so far the *Triticale* is the only cereal amphiploid which may be of value as a crop in Agriculture, there is no doubt of the importance of other types of amphiploids as research material in breeding programmes. So, amphiploids of type *Triticum-Triticum, Triticum-Agropyron, Triticum-Aegilops, Triticum-Haynaldia,* etc. (ARMSTRONG and McLEMAN, 1944; BELL, 1950; BELL, LUPTON and RILEY, 1955; JENKINS and MOCHIZUKI, 1957; MOCHIZUKI, 1943; PETO and BOYES, 1940; RILEY and CHAPMAN, 1957; SEARS, 1939b, 1941a, 1941b; SIMONET, 1953; ZHEBRAK, 1939 to 1944; etc.) have been synthesized since RAW (1939) obtained the first fertile amphiploids of *Triticum-Agropyron* type.

In the genus *Avena* studies have been also carried out concerning the possibilities of obtaining and applying to Oat Breeding amphiploids involving the species *A. sativa, A. abyssinica, A. strigosa* and *A. barbata* (CAMERON and GARVIN, 1952; BROWN and SHANDS, 1954; ZILLINSKY, 1955; all of them cited by O'MARA, 1961).

b) *Chromosome addition lines.*

The lack of adaptation of the genomes involved in the amphiploids to their new status prevents immediate utilization in Agriculture. To overcome this, O'MARA (1940, 1951) devised a method by which favourable characters of rye could be incorporated into wheat avoiding the problems of low fertility, genome interaction, etc., of *Triticale.* By this method he obtained plants whose cells had the complete chromosome complement of wheat plus one pair of homologous rye chromosomes. These individuals constitute the disomic chromosome addition lines. Using techniques more or less similar to O'Mara's technique, HYDE (1953) got five addition chromosome lines from *Haynaldia villosa* to wheat; SEARS (1956) synthesized from *Aegilops umbellulata* to wheat; SADANAGA (1957) was the first to obtain a rye chromosome addition line in tetraploid wheat; RILEY and CHAPMAN (1958) synthesized four addition lines from rye to wheat; EVANS and JENKINS (1960) the complete series of rye addition lines; MOCHIZUKI (1960, 1962), the complete series of *Agropyron* to tetraploid wheat; and so on.

Owing to the fact that chromosome addition lines are not quite stable, as shown by Riley and his collaborators in rye-wheat addition lines, monosomic addition lines are present in the offspring of disomic addition lines. In turn, monosomic addition lines segregate to 42-chromosome forms in which rye chromosomes are absent. Therefore, rye chromosome present in addtion lines should be carrier of gene or genes controlling characters with a great selective advantage in Evolution or Agriculture so that they are not lost in successive generations.

In consequence, chromosome addition lines do not seem to be of value as cultivated forms, although they are very valuable material for both theoretical studies and techniques such as gene transfer.

c) *Alien chromosome substitution lines.*

Going on with the purpose of introducing alien variation in a more stable and advantageous way, substitution lines, in which one pair of homologous chromosomes are replaced by another pair from an individual belonging to different species, are produced.

So far, studies made both on chromosome addition and substitution lines in cereals are only concerned with wheat, but it is to be expected that in the near future similar investigations may be made in oats.

Since there is affinity between certain basic genomes ($x = 7$) within *Triticinae,* it is logical to think of the great utility for Cereal Breeding of using interspecific or intergeneric chromosome substitution lines.

O'MARA (1947) studies the effect of substituting a specific rye chromosome for a specific wheat chromosome. Nulli-IX plants of *Triticum aestivum* are completely male sterile, largely female sterile and weak. Adding a rye chromosome in the disomic condition to nulli-IX wheat individuals, male fertility is restored, female fertility increased and the vigour of the plants appears normal. The above addition is equivalent to substituting the pair of *Secale* chromosomes for chromosome IX of wheat. It is interesting to point out that this effect is different from that of adding the pair of chromosomes to complete genome of common wheat because these plants (42 wheat chromosomes plus 2 rye chromosomes) are semi-dwarf and partially female fertile ones.

It is concluded that from the behaviour of an addition line it cannot be predicted those of the substitution lines which correspond to the specific rye chromosome.

Later, JENKINS (1956) devised a method to substitute in a systematic way the rye chromosomes in wheat complement.

The greater utility of rye chromosome substitution lines in wheat when compared with the addition lines may be due to their better genetic equilibrium and chromosome stability in successive generations. If rye univalents occur as a consequence of meiotic irregularities, gametes lacking the rye chromosome will be formed. When this happens in addition lines, the gamete deficient for rye chromosome will have the complete haploid set of wheat chromosomes; therefore, it will be quite functional. But in the case of substitution lines, the rye chromosome deficient gametes will have not the haploid set of chromosomes of wheat and, as a consequence, they will compete to disadvantage with the pollen of *n-1* wheat + *1* rye chromosomes (RILEY).

Hitherto, not any chromosome substitution lines haven been used in Agriculture as cultivated forms, but it may be expected in the near future.

d) *Gene transfer.*

We have seen that the techniques to introduce alien variation in cultivated plants from more or less related species show a gradual reduction of the genetic material with which the non cultivated species contributes. This reduction is made in order to avoid as much as possible meiotic irregularities and their consequent chromosome instability.So that, from amphiploids in which complete alien genomes are added to that of cultivated species, passing through chromosome addition and substitution lines, the alien chromatin material incorporated into wheat genome has been minimized by intercalating small portions of the alen chromosome. These portions carrying the gene or genes conditioning the favourable characters which are desired to transfer to wheat.

By radiating plants of wheat to which one chromosome of *Aegilops umbellulata* carrying the gene or genes conditioning leaf rust resistance (*Puccinia rubigovera*) had been added, SEARS (1956) was able to intercalate within a wheat chromosome a segment of *Aegilops* chromosome carrying such genes. KNOTT (1961), radiating a monosomic chromosome addition line of wheat involving one *Agropyron elongatum* (HOST) BEAUV chromosome, transferred the stem rust resistance from *Agropyron* to wheat. DRISCOLL and JENSEN (1963) studied a method to detect and isolate ryewheat intergeneric translocations induced by radiation. The same authors (DRISCOLL and JENSEN, 1964) were able to transfer leaf rust resistance from rye to wheat.

e) *Gene recombination.*

With the techniques devised by cytogeneticists and cereal breeders in order to introduce alien variation in cultivated species, it had not been possible to obtain —as a consequence of crossing-over— gene recombination between hereditary material of the cultivated species and that from related species. It is due to lacking meiotic pairing between chromosomes of different species because of their non-homology.

Introgression phenomenous are not frequent. SÁNCHEZ-MONGE (1958b) cited introgression of rye genes into wheat. Nevertheless, this fact has no value as a systematic method in any breeding programme.

RILEY and CHAPMAN (1958b) and SEARS and OKAMOTO (1958) showed that in plants of common wheat defficient for chromosome V (5B) there was non-homologous pairing and multivalents were formed. Subsequently RILEY and KEMPANNA (1963) demonstrated that this non-homologous pairing resulted in recombination between homoeologous chromosomes, that is between genetically equivalent chromosomes of the three component genomes of common wheat. Likewise it was showed that no other chromosome of the *Triticum aestivum* genome performs a similar control on meiotic affinity between homologous chromosomes (RILEY, CHAPMAN and KIMBER, 1960). RILEY (1960) demonstrated that genetic structure regulating this activity is restricted to the long arm of chromosome V (5B); and KIMBER (1964) pointed out the possibility that only one gene is responsible for the suppression of the meiotic affinity of homoeologous. Naturally, the locus of that gene being located in the long arm of the chromosome V (5B).

This series of linked together findings is one of the most very valuable contribution of Cytogenetics to Cereal Breeding. Meiotic pairing between chromosomes of both parents in certain hybrids when chromosome V (5B) is absent was demonstrated by RILEY, CHAPMAN and KIMBER (1959). Utilization of amphiploids deficient for such a chromosome will be of the greatest interest because fertile plants can be obtained in which interspecific gene recombination takes place as a consequence of meiotic pairing between chromosomes of different species (RILEY and

Chapman, 1963). In this way wheat breeders will be able to look for genetic variation from sources thus far inaccessible for them.

4. INTERVARIETAL SUBSTITUTION

Chromosome intervarietal substitution may be one of the most effective cytogenetic methods in Breeding of allopolyploid species, such as cultivated wheat and oats are.

For example: Welsh and Hehn (1964) have pointed out the importance of chromosome XVII (1D) concerning the milling quality of bread wheats. Undoubtedly, the substitution of chromosome XVII (1D) of a high-yield variety having bad milling quality by the same chromosome of a high-quality variety will be profitable for Agriculture.

The horizons open to investigation in this field are enormous. Techniques and methods followed to substitute the chromosomes of a variety by those of another one are known and they will not be detailed here. It may be convenient to emphasize the importance of forming stocks of complete monosomic series in a large number of commercial varieties in order to dispose of the aneuploid material which may be necessary in the breeding programmes.

In the conventional methods of Breeding by crossing, one begins with an initial cross between two varieties to select after in the segregant generations the plants showing a favourable gene combination. If it is wanted to gather in one combination a large number of genes, the probability of obtaining the desired genotype is very small because gene recombination is made at random. In addition, the time required to obtain a new commercial variety is excessively long, thus hindering the giving of flexibility to the obtention of new varieties which may respond to Agriculture necessities at any given moment.

Cytogenetic techniques for obtaining intervarietal substitution lines as new commercial varieties permit the minimization of the random participation. On the other hand, since not so large populations are handled as in the case of segregant generations of conventional methods, it is feasible to use embryo culture techniques and grow the material in control cabinets. On using these two techniques, the time required to obtain a new variety is very short, thus giving more plasticity to the perfomance of commercial varieties according to Agriculture requirements.

The monosomic series established by Sears in the common wheat variety *Chinese Spring* has been the corner-stone on which the chromosome intervarietal substitution techniques have developed.

The methods devised by SEARS (1953) and UNRAU, PERSON and KUSPIRA (1956), to produce intervarietal substitution lines have been followed by a number of investigators (SNYDER, LARSON, JENKINS, KNOTT, RILEY, LAW, among others). Law's work (LAW, 1964), in which he studied the interactive effects between substituted chromosomes and the recipient background, points out the importance of theoretical studies which are necessary before the practical value of intervarietal substitution lines may be assessed (RILEY, 1965).

In addition to studies on disease resistance made by means of intervarietal substitution lines (SEARS, LOEGERING and RODENHISER, 1957; GREEN, *et al.* 1960; KNOTT and SHEN, 1961 among others), the effects produced on quantitative characters such as earliness, height, 1000 kernel-weight, yield, etc., have been studied (KUSPIRA and UNRAU, 1957).

5. GENOME EXTRACTION AND CONSTRUCTION

The handling of genomes as a whole can also result very useful in allopolyploid species breeding.

KERBER (1964) studies the effect produced on isolating the tetraploid component (genomes A and B) in two varieties of hexaploid wheat (genomes A, B and D), using a simple technique of backcrossing and further selection of forms having $14^{II} + 7^{I}$ in Metaphase I of PMCs.

Although the tetraploid forms derived from hexaploid plant seem not to have good agronomic characteristics, there is no doubt that its genetic «skeleton» may be of value for further breeding programmes. The autor is carrying out a similar line of work at the Experimental Station of Aula Dei.

MOCHIZUKI and SHIGENAGA (1964) devised two theoretic procedures for the extraction of B genome from hexaploid wheat.

The *Analytic Breeding* of polyploid species has been theorized by CHASE (1962). This breeding technique consists of three phases: (a) reduction of the polyploid to its basic genomes (analysis), (b) breeding and selection to diploid level, and (c) resynthesis and test of the polyploid forms. Later, CHASE (1964) outlined what the *wheat analytic breeding* could be. This new cytogenetic breeding method has not been yet performed in practice.

Looking for the answer to the question if the genome of 7 chromosomes, characteristic of species included in tribu *Hordeae* (*Triticeae* Dumort, according to BOWDEN's review (1959)) is the minimal functional unity of the tribu, EVANS (1964) synthesized hexaploid plants ($2n = 42$) having the A and B genomes of durum wheat and a third genome constituted by *Aegilops* and *Agropyron* chromosomes in diverse rates. These hexaploid derivatives had a meiotic stability similar to that of *Triticum durum-Aegilops squarrosa* and *T. durum-Agropyron elongatum* amphiploids from which they arose. They showed characteristics of the three component species.

Genome analysis made by UPADHYA and SWAMINATHAN (1963) in a hexaploid wheat from Georgia (USSR) points out the possibility of having been originated by chromosome doubling of the hybrid *Triticum timopheevi* x *T. monoccocum*; that is, it would be a hexaploid wheat having a genome formula other than AABBDD.

The possibility of synthesizing new species by combining diverse genomes has undoubtedly, in addition to the theoretic interest, a great value for plant breeders.

From different points of view, UNRAU (1958), UNRAU and MCGINNIS (1958), BISHOP (1963) and RILEY (1965), have also reviewed applications of Cytogenetics to Plant Breeding.

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SUMMARY

A review of applications of Cytogenetics to cereal Breeding is made. The outstanding cytogenetic findings related to breeding of wheat, barley, oats and rye are outlined.

A number of lines of work can be found in a cytogenetic breeding programme. Such lines are:

1. Changes in ploidy level:
   a) Polyploidy (fertility and aneupolyploidy).
   b) Haploidy.

2. Chromosome aberrations:
   a) Sructural changes (translocations, duplications, etc.).
   b) Changes in number of chromosomes (aneuploidy).

3. Introduction of alien variation:
   a) Hybrids and their amphiploids.
   b) Chromosome addition lines.
   c) Chromosome substitution lines.
   d) Gene transfer.
   e) Gene recombination (genetic control of meiotic pairing: Chromosome V (5B)).

4. Intervarietal chromosome substitution.

5. Genome extraction and construction.

RESUMEN

Se hace en este artículo una revisión sobre las aplicaciones de la Citogenética a la Mejora de los cereales, describiéndose los descubrimientos citogenéticos más importantes y que están relacionados con la mejora de trigo, cebada, avena y centeno.

En un programa de Mejora Citogenética de dichos cereales se pueden seguir numerosas líneas de trabajo, tales como:

1. Cambios en el nivel ploídico:
   a) Poliploidía (fertilidad y aneupoliploidía).
   b) Haploidía.

2. Aberraciones cromosómicas:
   a) Cambios estructurales (translocaciones, duplicaciones, etc.).
   b) Cambios numéricos (aneuploidía).

3. Introducción de la variación extraespecífica:
   a) Híbridos y sus anfiploides.
   b) Líneas de adición cromosómica.
   c) Líneas de sustitución cromosómica.
   d) Injerto cromosómico.
   e) Recombinación génica (control genético del apareamiento meiótico: El cromosoma V (5B)).

4. Sustitución cromosómica intervarietal.

5. Extracción y construcción genómicas.

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