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Cytogenetics and Wheat Breeding

Citogenetika i oplemenjivanje pšenice

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Cytogenetics and Wheat Breeding

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Introduction

Wheat improvement by breeding consists of conscious direction of the evolution of the crop into the production of genotypes that cause phenotypic expressions more suited to agricultural exploitation than those previously available. As conventionally practised — by intervarietal hybridization followed by selection, or by intervarietal hybridization followed by backcrossing — wheat breeding copies some of the processes that give rise to evolutionary changes in nature. However, natural evolution is also accomplished by means other than segregation, recombination and selection which wheat improvement normally uses. For example evolutionary differences are also known to arise by polyploidy and aneuploidy, by chromosome structural changes, by the introgression of genetic material from one species into another, by modifications of breeding systems and by the elaboration of chromosomal mechanisms, as well as by mutation and selection.

We may therefore ask whether more versatility of method might usefully be employed in directing the evolution of wheat for agricultural purposes. The answer to this question depends upon two requirements:

1) That the procedures to be used make available genetic variation that was unattainable or difficult to manage by normal methods.
2) That appropriate techniques are available that can be applied to the problem.

So far as the usefulness of innovations in breeding methods are concerned, there can be no doubt that there is much valuable genetic variation that is either inaccessible by conventional means or is extremely difficult to handle. Moreover, even in dealing with the kind of beneficial variation made available by standard intervarietal hybridization programmes, the conventional procedures lack precision and this could be increased by alternative methods.

In considering the cytogenetic manipulations that are available for these purposes a number can be mentioned, all potentially capable of contributing to the agricultural evolution of wheat. Among these are intervarietal whole chromosome substitutions (Sears, Loegring & Rodenhiser, 1957; Kuspira & Unrau, 1957; Law, 1966), alien chromosome aditions and substitutions (O'Mara, 1940; Riley & Chapman, 1958a; Riley, 1960a), transfers of segments of alien to wheat chromosomes by induced translocations (Sears, 1956; Riley & Kimber, 1966) and the introduction of alien genetic variation by recombination following interference with the restriction of homoeologous meiotic pairing by chromosome 5B (Riley, 1960b; Riley & Kimber, 1966).

In order to indicate the potentialities of some of these methods I will now outline ways in which they are being used at Cambridge by Victor Chapman and myself, and by my colleagues Colin N. Law and Gordon Kimber. My purpose is, by selecting a number of examples from our current programmes, to illustrate some of the possibilities made available by current cytogenetic knowledge in wheat since I cannot in the space available undertake a comprehensive survey. However a more detailed treatment of the subject can be found in the work of Riley & Kimber (1966).

Intervarietal chromosome substitutions and wheat breeding

The first series of 21 lines, in which every chromosome of the complement of *T. aestivum* was monosomic in turn, was established by Sears (1953, 1954) in the variety Chinese Spring. Following the development of the Chinese Spring series, Sears (1953) and Unrau (1950) showed that new series could be created in any other variety by a simple backcrossing procedure. In this crossing programme the Chinese Spring monosomics are used as the non-recurrent parents and the alternative variety as the recurrent parent.

Moreover, the monosomic lines, in any variety, can be used to produce intervarietal substitution lines in which chromosomes of the monosomic — recipient — variety are replaced by corresponding intact pairs from a donor variety. This is achieved by a backcrossing procedure in which the recipient monosomic lines are the recurrent parents and the donor variety is the non-recurrent parent. Substitution lines were first developed in this way by Sears, Loegring & Rodenhiser (1957), and others have been produced at Cambridge by my colleague, Dr C. N. Law.

Among the material developed at Cambridge has been a full set of 21 substitutions in which every chromosome pair of the variety Cappelle-Desprez, in turn, replaces its homologue in Chinese Spring. Particular interest attaches to this substitution series because the resistance to eyespot *(Cercosporella herpotrichoides)* of Cappelle-Desprez contrasts strikingly with the susceptibility of Chinese Spring.

Cappelle-Desprez has been pre-eminent among the winter varieties used in British agriculture for a number of years and its success can probably be ascribed in part to its eyespot resistance (Macer, 1964). Cappelle-Desprez was derived from a cross between the resistant variety Hybride du Joncquois and the susceptible variety Vilmorin 27.

Table 1

SCORES FOR THE REACTION TO EYESPOT (CERCOSPORELLA HERPOTRICHOIDES OF THE LINES IN WHICH THE CHROMOSOMES OF CAPPELLE-DESPREZ ARE SUBSTITUTED FOR THEIR HOMOLOGUES IN CHINESE SPRING

Chromosome substituted	Score More susceptible than Chinese Spring	 Like Chinese Spring	 Like Cappelle-Desprez
1A	—	118.7	—
1B	—	101.7	—
1D	—	70.7	—
2A (II)	180.2	—	—
2B (XIII)	—	155.5	—
2D	—	93.3	—
3A	—	112.8	—
3B	—	135.0	—
3D	—	96.9	—
4A	—	105.1	—
4B	—	94.3	—
4D	—	117.2	—
5A	—	94.1	—
5B	—	78.5	—
5D	—	120.7	—
6A	—	130.2	—
6B	—	—	47.8
6D	—	—	27.6
7A	—	—	49.8
7B	—	146.5	—
7D	—	106.5	—
Chinese Spring	—	114.7	—
Cappelle-Desprez	—	—	54.9

Moreover, Hybride du Joncquois was also a parent of another resistant variety — Viking. In addition, the cross Cappelle-Desprez × Holdfast has given rise to a resistant variety — Maris Widgeon. The apparent ease of transmission of eyespot resistance — from Hybride du Joncquois to Cappelle-Desprez and Viking, and from Cappelle-Desprez to Maris Widgeon — suggests that it is relatively simply inherited. However, it has not been possible to determine the mode of inheritance because resistance is difficult to detect in individual plants, although it can be recognised readily on a population scale.

Since intervarietal chromosome substitution lines are homozygous and can be accumulated into populations of any size it seemed worthwhile to study the resistance to eyespot of the Chinese Spring — Cappelle-Desprez lines. When this was done the lines in which chromosomes 6D, 6B and 7A of Cappelle-Desprez were substituted into Chinese Spring were found to be much more resistant than Chinese Spring and to possess levels of resistance approaching or even greater than, that of Cappelle-Desprez (Table 1) (Law, Macer & Riley, unpublished). By contrast the line, in which chromosome 2A of Cappelle-Desprez was introduced, was more susceptible than the recipient Chinese Spring. That chromosome 2A apparently increases the susceptibility of Cappelle-Desprez is comprehensible when it is appreciated that Hybride du Joncquois, one of its parents, has a higher level of resistance than Cappele-Desprez.

Apparently, therefore, resistance to eyespot is determined in a relatively simple manner in Cappelle-Desprez. Moreover, this study has shown that a considerable level of resistance can be transferred to any other variety simply by substituting from Cappelle-Desprez one of the chromosomes whose activity is responsible for resistance. The transfer can be achieved without any necessity for testing for disease resistance during the backcrossing programme because the chromosome acts as a marker for the resistance gene or genes. A rational approach to breeding for eyespot resistance is therefore provided by the use of substitution procedures.

Clearly there is an operational advantage to the use of intervarietal chromosome substitutions when handling qualitative genetic effects of poor penetrance, such as eyespot resistance. However, the practical value of breeding procedures of this kind are as yet relatively unexplored and it may be that they will ultimately prove to be of even more importance in improving quantitatively inherited characters. Hints of this are contained in the work of Kuspira & Unrau (1957) which showed that even expressions of yield can be advanced by the replacement of a single chromosome pair. It is of the greatest importance that chromosome substitutions should be studied between varieties both of which are adapted to the agriculture of the region where the work is being conducted. Until this is done we shall not fully comprehend the significance of the new weapon with which cytogenetics has armed the wheat breeder.

Resistance of Aegilops ventricosa to Cercosporella herpotrichoides

Before turning to the transfer of alien variation to wheat by disruption of the activity of chromosome 5B in order to obtain appropriate recombinants, I would like to discuss a comparatively conventional programme that is being carried out by my colleague, Dr. Gordon Kimber. This involves the attempt to incorporate in *T. aestivum* the outstanding resistance to eyespot*(Cercosporella herpotrichoides)* of *Aegilops ventricosa* ($2n = 28$).

Ae. ventricosa is an allotetraploid species which was shown by the analyses of Kihara (Lilienfeld, 1951) to have the genome constitution DDM^vM^v. The D genome is homologous with one of the genomes of *T. aestivum* while the M^v genome is not homologous with any of those of wheat. If the resistance to eyespot is simply inherited — controlled by one or few genes — the ease or difficulty of the transfer of the resistance to wheat will be determined by their location. Resistance could be introduced with ease into wheat by recombination if it is determined by the D genome, but if it is determined by the M^v genome more complex problems would be posed. The necessity might then be created of making alien chromosome addition lines and perhaps of using 5B-breaking systems.

In the work at Cambridge the 56-chromosome amphiploid *T. turgidum* × *Ae. ventricosa* ($AABBDDM^vM^v$) was first created. This was crossed with *T. aestivum* to make 49-chromosome AABBDDM^v hybrids. After two backcrosses to *T. aestivum,* accompanied by selection for eyespot resistance, plants have been isolated, with resistance comparable to that of *Ae ventricosa,* which form 21 bivalents at meiosis.

From this it can be concluded that the resistance is determined by a gene or genes on D genome chromosomes and that appropriate recombination has taken place resulting in the transfer of the critical genes to wheat chromosomes. Dr. Kimber is now working to incorporate the *Ae. ventricosa* resistance in agriculturally acceptable genotypes. It is clear that a number of further backcrosses to *T. aestivum* will be needed to separate the resistance from a number of undesirable attributes derived either from *T. turgidum* or *Ae. ventricosa.*

However, this exercise illustrates rather nicely that characters of profound agricultural significance can be introduced from remote relatives into wheat by conceptually simple, though operationally cumbersome, procedures. The processes involved are those of introgressive hybridization that have been vividly described from nature by Anderson (1949). The only complicating addition to the natural evolutionary sequence was the creation of a synthetic amphiploid to bridge the sterility barrier between the *Aegilops species* and wheat.

Interference with the 5B system

1. **The absence of chromosome 5B.** — There are many species, related to wheat, that possess genetic attributes that would be agriculturally beneficial if transferred to the crop plant. Such useful genetic variation is found for example in the genera *Aegilops, Secale* and *Agropyron.* However, it is often inaccessible to the wheat breeder because, in hybrids between the alien species concerned and *T. aestivum,* there is no meiotic pairing and recombination between chromosomes derived from different parents. Consequently alien genes cannot be transferred to wheat chromosomes by recombination and there is thus a meiotic barrier to the utilization of valuable genetic variation.

A means of surmounting this meiotic barrier was proposed by Riley & Chapman (1958b) on the discovery that a genetic activity of chromosome 5B is responsible for the meiotic isolation of homoeologous chromosmes in *T. aestivum.* It was reasoned that the same genetic activity might also be responsible, in hybrids, for the absence of meiotic pairing and crossing-over between the chromosomes of wheat and those of the other parent.

This hypothesis was tested by Riley, Chapman & Kimber (1959) using 28- and 27-chromosome hybrids between *T. aestivum.* monosomic 5B (2n = 41) and *Ae.longissima* (2n = 14). There was high pairing at meiosis, with numerous trivalents and quadrivalents, in the 27-chromosome 5B-deficient hybrids whereas in the 28-chromosome hybrids, carrying 5B, there was very little pairing. The nature of the pairing in these 5B-deficient hybrids, and in many others that were subsequently examined involving wheat and a range of different alien species (Riley & Law, 1965), was such that it could be concluded with certainty that wheat chromosomes paired, and therefore recombined, with those of the alternative parent. The absence of the genetic activity of chromosome 5B therefore removes the obstacle to the introduction of alien genetic variation into wheat by meiotic recombination.

As an example of breeding research in which the deficiency of 5B has been studied I shall discuss the derivatives of the cross *T. aestivum* var. Holdfast monosomic 5B × *Aegilops bicornis* ($2n = 14$). *Ae. bicornis* is a primitive annual grass, of south eastern coastal areas of the Mediterranean, which has no attributes of obvious agricultural worth. However we chose to work with it as an exercise in the handling of 5B-deficient hybrids and their derivatives.

The initial hybrids had 27 chromosomes and displayed a considerable amount of allosyndetic pairing at meiosis, although this does not occur in otherwise similar 28-chromosome hybrids carrying 5B. The F_1 hybrids were entirely self-sterile, but when pollinated by Holdfast gave a few seeds from which first backcross plants were grown. These had 35 chromosomes and chromosome 5B had been restored in the contribution of the recurrent parent. However, at meiosis several trivalents and quadrivalents were commonly formed, presumably due to heterozygosity for structural changes that had arisen by homoeologous recombination at the F_1 stage. These plants were also self-sterile and were pollinated with Holdfast.

The resulting second backcross generation contained plants with a range of chromosome numbers, some of which approached the euploid number of 42. A good deal of structural heterozygosity still remained, but all the plants were self-fertile and no further backcrosses were made.

After three further generations of selfing many derivatives had returned to a 42-chromosome state and were more or less regular meiotically, although varying levels remained of structurally heterozygosity — the residue of interchanges produced by homoeologous recombination at the F_1 stage. When these derivatives were check crossed with Holdfast the resulting hybrids usually formed 21 bivalents — although there were sometimes marked reductions in the level of meiotic pairing relative to that of the parents. Most derivatives of the programme therefore carried 21 pairs of chromosomes homoeologous, at least in part, with the 21 pairs of Holdfast.

However, in only a few instances did the phenotypes of the derivatives correspond with that of Holdfast, the only *T. aestivum* parent involved in the programme. The phenotypic changes must, therefore, be ascribed to the presence of segments of the chromosomes of *Ae. bicornis* that were incorporated in wheat chromosomes by allosyndetic recombination in the initial 5B-deficient hybrids. It seems reasonable to presume that it is the presence of these alien segments that occasionally interupt meiotic pairing in hybrids between Holdfast and the 42-chromosome products of the Holdfast—*Ae. bicornis* breeding programme.

The phenotypic changes, resulting from the incorporation of genetic material of *Ae. bicornis* in Holdfast, range from the modifications of such qualitative characters as mildew resistance and grain colour to the alteration of quantitative attributes such as height, earliness, ear conformation, grain size and yield. Perhaps the most surprising outcome of this work has been the demonstration that characters of agronomic importance can be changed in a potentially useful manner by breeding from 5B-deficient hybrids between wheat and such an apparently unpromising parent as *Ae. bicornis*. However, Table 2 shows the results of a small scale experimental trial consisting of three replications, with plots each of four rows eight feet long, which were sown with seeds at two inch spacings. The *Ae. bicornis* derivatives in this experiment were all stabilized at approximately the 42-chromosome euploid level and it will be seen that a range of yields occurred of which two were higher than that of Holdfast. Moreover selection 17/21/18 had a significantly greater yield than Holdfast and it also exceeded Cappelle-Desprez, although not significantly.

Table 2

YIELD OF SOME DERIVATIVES OF THE CROSS T. AESTIVUM HOLDFAST MONOSOMIC 5B × AE. BICORNIS

	Selection	Mean yield per plot (gms)
	Cappelle-Desprez	767.67
	Holdfast	691.46
Ae. bicornis derivatives	3/13/ 7	626.80
	15/ 5/11	720.63
	15/17/ 7	473.23
	17/ 4/15	673.87
	17/15/11	702.80
	17/21/18	794.13
	17/24/ 1	464.37
	Standard error	39.20

I am not suggesting that there is a great likelihood of new varieties, of immediate agricultural value, arising directly from the kind of programme described, although this is not impossible. However, it is quite clear that valuable parental material can be obtained, indeed this work has given a new dimension to the employment of alien genetic variation in wheat improvement. Hitherto wide-crossing has been primarily thought of in relation to the transfer of limited, simply inherited, characters to wheat. It is now clear that useful changes of quantitatively inherited agronomic characters can also result.

More importantly, however, this study has shown the feasibility of transferring genetic variation from related species to wheat by interference with the 5B system. As a consequence the original proposals concerning these methods are confirmed and the range of genetic variation available for inclusion in wheat improvement programmes is greatly extended.

2. **Genetic suppression of the activity of chromosome 5B.** — The second example that I shall discuss of interference with the 5B system concerns recombination between wheat and alien chromosomes induced by genetic suppression of the 5B activity. The possibility of doing this arose from the hypothesis that the high level of meiotic pairing in hybrids between *T. aestivum* and *Aegilops speltoides* (2n = 14) resulted from the suppression by the *Ae. speltoides* genotype of the activity by which homoeologous pairing is normally inhibited in wheat (Riley, Kimber & Chapman, 1961). The hypothesis was tested by making *T. aestivum* × *Ae. speltoides* hybrids in which two distinct wheat chromosomes were simultaneously marked by telocentric conditions. At meiosis in the hybrids the two telocentric chromosomes never participated in the same configuration when they were not homoeologous, but homoeologous paired together in the same configurations (Riley & Chapman, 1964, 1966). The hypothesis was therefore confirmed and it was apparent that, since the chromosome 5B activity was suppressed in the presence of the *Ae. speltoides* genotype, this effect could be used to promote recombination between wheat and alien chromosomes in a manner analogous to the use of 5B-deficiency conditions.

This approach is being used in attempts to transfer to *T. aestivum* the high level of resistance (hypersensitivity) of *Aegilops comosa* (2n = 14) to stripe rust *(Puccinia striiformis)*. Initially 28-chromosome hybrids were produced from the cross. *T. aestiwum* Chinese Spring × *Ae. comosa* and these were pollinated by Chinese Spring. After a number of further backcrosses to Chinese Spring, accompanied by selection for stripe rust resistance, a 43-chromosome resistant line was isolated. This had 21 bivalents and one univalent at meiosis, and after self-pollination it gave rise to a resistant 44-chromosome line with 22 bivalents at meiosis. Hybrids between this line and Chinese Spring formed 21 bivalents and one univalent at meiosis, so that the parental line clearly carried disomically the chromosome of *Ae. comosa* responsible for stripe rust resistance. Subsequently by a genetic test the *Ae. comosa* chromosome was found to be capable of substituting with good compensation for all three pairs of chromosomes of homoeologous group 2, but for no other wheat chromosomes (Riley & Chapman, unpublished). The *Aegilops* chromosome therefore corresponds in overall genetic activity to the chromosomes of homoeologous group 2.

However, under normal circumstances there was no indication of any meiotic affinity between this chromosome and any of those of the wheat complement. Consequently the gene or genes responsible for the resistance to stripe rust could not be transferred to a wheat chromosome by recombination without further manipulation. From a knowledge of the behaviour of 5B-deficient hybrids between wheat and *Ae. comosa* it was nevertheless clear that recombination would occur following interuption of the 5B effect (Riley & Law, 1965). Since there was no simple way of producing nullisomy for chromosome 5B in the disomic addition line it was necessary to atempt to exploit the suppressing activity of *Ae. speltoides.*

The 44-chromosome disomic addition line was therefore crossed with *Ae. speltoides* to produce 29-chromosome hybrids. It was reasoned that the suppression of 5B activity in these hybrids could lead to meiotic recombination between the *Aegilops comosa* chromosome and some of those of the wheat complement — probably in homoeologous group 2. The F_1 plants were self-sterile and were pollinated by Chinese Spring.

The resulting first backcross generation plants had either 34 or 35 chromosomes, and at meiosis made from six to ten bivalents, two to four trivalents and there were numbers of univalents. The trivalents in this generation, and trivalents and quadrivalents in subsequent generations, were presumably indicative of heterozygosity for translocations that had arisen by homoeologous recombination at the F_1 stage. The first backcross generation was entirely self sterile and was pollinated with Chinese Spring to give second backcross progenies, among which selection was practised for rust resistance.

The resistant plants had chromosome numbers ranging from 37 to 44 and at meiosis they were somewhat irregular with a maximum of one quadrivalent, two trivalents and five univalents. Some were self-fertile but all were again backcrossed to Chinese Spring. All the third backcross derivatives were selected for stripe rust resistance but since this is the stage now reached it is not possible fully to discuss their meiotic behaviour. However, resistant plants with 21 bivalents occur so that the stripe rust resistance of *Ae. comosa* has been transferred to wheat.

I hope that a sufficient description has been given to illustrate the approach being adopted at Cambridge to introduce alien variation into wheat following genetic suppression of the 5B effect. Obviously it is too early to be sure that the method will be completely successful. More backcrossing and selection will be needed before we can be certain that 21 pairs of wheat chromosomes can be retained together with the stripe rust resistance of *Ae. comosa.* Nevertheless on theoretical grounds there is every prospect of success and, whether or not it is achieved in the present experiment, a new procedure has been added to the repertoire of the wheat breeder-cytogeneticist. The procedure will have its uses whenever, as in the present circumstances, it is not possible to work from a 5B-deficient situation and yet homoeologous pairing is required.

Conclusion

Following this brief examination of four programmes in which cytogenetics is being applied to wheat breeding, perhaps the most important conclusion I should draw concerns attitudes taken to breeding research. Wheat cytogenetics is advancing rapidly and as new knowledge becomes available novel approaches can be made to the improvement of the crop. It seems to me to be important that our attitudes should be adventurous, that we should all be prepared to use the new methods where they can be appropriately employed. For in *T. aestivum* we have an organism of remarkable genetic flexibility. The flexibility should be exploited to speed the agricultural evolution of wheat, for the need for more closely adjusted genotypes is greater than ever.

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Citogenetika i oplemenjivanje pšenice

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Rezime

Razvoj citogenetike pšenice je sada već dostigao stadij kad kontrola hromosomske konstitucije selekcionog materijala može znatno doprineti korišćenju genetske varijabilnosti. U oplemenjivačku proceduru može se uneti veća preciznost nego što je to bilo ranije moguće, a genetska varijabilnost vrsta srodnih sa pšenicom može se preneti u pšenicu, što je dosada bilo nedostižno.

U prvom redu može se istaći zamena hromozoma između raznih sorti unutar Triticum aestivum. Vrednost takvog materijala može se pokazati na primeru otpornosti prema Cercosporella herpotrichoides, jednoj opasnoj bolesti u zapadnoj Evropi. Stvorena je potpuna serija od 21 linije u kojima je svaki hromosom od otporne sorte Cappelle-Desprez zamenjen u osetljivoj sorti Chinese Spring. U jednoj supstitucionoj liniji, puna otpornost Cappelle-Desprez je unesena u Chinese-Spring, tako da je ta otpornost očigledno određena u prvom redu aktivnošću jednog hromosoma. Prenošenje otpornosti u bilo koju osetljivu sortu sada je jedino stvar supstitucije kritičnog hromosoma od Cappelle-Desprez.

Otpornost prema C. herpotrichoides takođe daje model za proceduru uvođenja strane genetske varijabilnosti u pšenicu. Aegilops ventricosa (2n-4 ×-28) koja ima genome DDM^vM^v poseduje tip otpornosti prema C. herpot. superiorniji nego bilo koji drugi sada raspoloživi kod pšenice. Amfidiploid T. turgidum × Ae. ventricosa je ukršten sa T. aestivum i nekoliko povratnih ukrštanja je izvedeno sa T. aestivum kao roditeljem primaocem. Na kraju su izdvojene 42-hromosomske biljke koje su imale 21 bivalent u mejozi i bile otporne prema C. herpot. Prema tome, otpornost je uslovljena jednim genom ili genima na hromosomima D genoma i ova otpornost može se iskoristiti u oplemenjivanju pšenice.

Prva zapreka unošenju mnogostrane genetske varijabilnosti u pšenicu je uzrokovana odsustvom mejotičkog parenja i rekombinacije između hromosoma pšenice i tih drugih vrsta s kojima se ukršta. Ova zapreka se može savladati odstranjivanjem hromosoma 5B ili sprečavanjem genetske aktivnosti toga hromosoma. Poznavanje ovog sistema je korišćeno kod prenošenja otpornosti prema Puc. striiformis od Aegilops comosa.

Rekombinacije usled deficije hromosoma 5B u interspecies hibridima se takođe mogu koristiti u modificiranju kvantitativnih svojstava. Na primer, uvođenje na ovaj način varijabilnosti od Aegilops bicornis u pšenicu je rezultiralo u potencijalno korisnim modifikacijama takvih agronomskih svojstava kao što je prinos.

DISCUSSION

I. ZONJIĆ (Beograd): *I would like to know whether Dr Riley has obtained the lines in which the substitution of genes from Aegilops to Agropyron has been made, what can be of great importance for wheat breeding?*

R. RILEY (England): *Yes Dr Zonjić, we have isolated useful breeding material incorporating characteristics of Aegilops species. It is now clear that the reservoir of genetic variations that can be exploited in wheat breeding has, been extended to include Aegilops, Agropyron and pehaps Secale.*