EARLY GENERATION TESTING AS A MEANS OF PREDICTING THE VALUE OF SPECIFIC CHROMOSOME SUBSTITUTIONS INTO COMMON WHEAT

by

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ABSTRACT

In an attempt to establish tests by which the value of whole chromosomes for substitution could be determined, two experimental methods were used. The first of these, the F_1 method, depended on the comparison of the performance of reciprocal F_1 monosomic x disomic hybrid combinations, in which the univalent chromosome from the two different sources was tested against the uniform genetic background provided by the F_1 hybrid. The second method, called the F_3 bulk method, involved the establishment of the chromosome pair under test in a pure state in a F_3 hybrid bulk by the use of the appropriate monosomic line. This material was tested against the F_3 hybrid bulk of the parental varieties in which all the chromosomes were freely segregating, and also against pre-existing substitution lines.

The F_1 method demonstrated marked differences between homologous chromosomes of different varieties when they were tested in the univalent condition for the characters investigated. From these differences the homologous chromosomes of the varieties could, in some cases, be arranged in a linear order of performance, an order which may indicate their relative contribution if they were used in the production of substitution lines.

The F_3 bulk method did not reveal appreciable differences between the chromosome lines studied and therefore could not be used as a predictive method.

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INTRODUCTION

In the breeding of self-fertilizing crop plants, the pedigree and bulk methods have become well established as the principal methods for the production of improved varieties. With the establishment of the complete series of monosomics in hexaploid common wheat, however, a new technique potentially of great value to wheat breeders has been evolved. This is the replacement or substitution of a single chromosome pair of one wheat variety by the homologous pair from another wheat variety. Results are already available which indicate that these substitutions can dramatically alter such characters of particular interest to the plant breeder as grain yield, earliness, plant height and protein content.

The method by which this chromosome substitution is accomplished is well established, but there remains a need for further investigation and testing of this method to confirm its usefulness as a plant breeding technique. If the substitution method is accepted as a possible wheat breeding method of the future, then a search for possible refinements of this method would seem to be the next step.

The procedure of chromosome substitution involves a series of backcrosses of the hybrid, to the recurrent parent in the monosomic condition so that the latter is reconstituted in a more or less pure state, while the substituted chromosome from the donor parent is retained intact as a univalent. The process of producing a chromosome substitution is therefore a slow one, involving a period of several years even under the most favourable conditions, and at its conclusion

there is no assurance that the combination obtained is the most satisfactory one possible, as the testing of the substitution line can only be effected when the backcross programme has been completed, and the substitution line stabilized in the disomic condition by selfing.

In view of this, any means of assessing the value of combinations of recipient varieties and substituted chromosomes prior to the commencement of the substitution would be of great value. By the use of such a test, the most favourable combination could be determined at the outset, and the risk of the ultimate product of the substitution being unsatisfactory would be minimized. It is towards this end that the following study has been directed.

The project, then, is concerned with two facets of plant breeding, the application of the monosomic wheat lines to the improvement of wheat varieties, and a further attempt to use early generation testing as an aid to plant breeding procedures.

LITERATURE REVIEW

Monosomics

The occurrence of aneuploids as cytological deviations from the normal chromosome number of a plant species or variety had been known and described long before they were put to a practical use as tools for genetical analysis or plant improvement. Early reports include the trisomics of Datura described by Blakeslee (5), McClintock's corn trisomics (26), and the monosomics of tobacco developed by Clausen and Cameron (6). The development of a complete series of monosomics in the tetraploid tobacco was a significant advance that foreshadowed the ultimate establishment of complete monosomic and nullisomic series, as well as the hyperploid series in the hexaploid wheat variety Chinese Spring by Sears (34, 35, 37).

It seems that the higher levels of ploidy can tolerate the absence of a whole chromosome, or even a chromosome pair, unlike the true diploid species in which whole chromosome deficiencies are not usually found. This is due no doubt to the replication of genetical material in the polyploids (35).

In the monosomic series in wheat, Sears was able by cytogenetical testing to number the chromosomes from I to XXI and assign them to their respective genomes, either the A, the B or the D. By further investigation the chromosomes were placed in homoeologous groups according to their probable phylogenetic relationships. This later work enabled Sears (38) to revise his numbering system from the Roman numerals to one identifying each chromosome by its homoeologous

group and genome, that is, from 1A to 7D.

After the monosomic series had been established in one variety, it was not difficult to produce additional series in other wheat varieties (46), and tests have also been designed using these deficient lines to assign genes for certain characteristics of the wheat plant to their chromosomes. Genetical information of this nature can be obtained directly from the nullisomic condition in certain "critical" lines of a variety, or from the "critical" lines in the F_1, F_2 or F_3 generations of crosses between the variety carrying the characteristic to be analysed and the monosomic series.

A further application of the monosomic wheat lines was found in their use in the technique of whole chromosome substitution, the method of which was described by Sears (36), and in greater detail by Unrau, Person and Kuspira (46). Besides being a further method of locating genes, particularly those affecting quantitative characters, the idea of replacing whole chromosomes had considerable appeal to some cereal breeders, for the work of Kuspira and Unrau (22) clearly demonstrated that such agronomically and economically important characters as yield, earliness, and protein content could be substantially changed in some cases by the replacement of a single pair of chromosomes. These workers investigated three sets of substitution lines, with the variety Chinese Spring as the recurrent parent and the substituted chromosomes from the donor varieties Thatcher, Hope and Timstein. These lines were studied in replicated block trials for up to three seasons and the effect of the substitution of a pair of chromosomes evaluated for a number of quantitatively inherited characters by determining the differ-

ence in performance between the substitution line and the recurrent variety Chinese Spring. The majority of these characteristics was found to be influenced by the genetic material contributed by at least several of the donated chromosomes. This study is of particular relevance to the project at hand, as the results that these workers obtained for certain substitutions will be the basis for an evaluation of the success of one of the early testing methods used. Kuspira and Unrau (22) considered the possible application of the substitution method to wheat breeding, and concluded that it may be valuable under certain conditions, while two recent plant breeding text books (2, 7) have also mentioned this possibility.

The substitution of whole chromosomes is not limited to intervarietal substitutions between bread wheats. O'Mara (20), for example, described the substitution of a specific pair of rye chromosomes for a pair of wheat chromosomes to produce vigorous and fertile plants in which the rye chromosomes apparently substituted effectively for the deficient wheat pair.

The possibility also exists for the substitution of chromosomes from other Triticum species or from such wheat relatives as Agropyron, Aegilops and Haynaldia into the hexaploid wheats, Jenkins (16). These alien substitutions may well confer new and interesting characteristics to the wheat, which the plant breeder will then be able to exploit.

Early Generation Testing

In the pedigree system of breeding self-pollinated crops any

appraisal of the material that would allow elimination early in the breeding programme of lines that would not produce the desired combinations, would be of great assistance to the plant breeder. Such a method would in fact involve an attempt to estimate the genotypic value of the subsequent segregates from the characteristics of the parental population. A number of independent investigations have been conducted to assess the validity of early generation testing. These studies have differed in a number of respects, the crop plant used for example, the precise aims of the investigation and the details of the experimental procedure, so it is frequently difficult to compare directly the results obtained or the conclusions drawn by the various authors.

In an early study of this nature, Harrington (13) attempted to establish the potential value of a wheat cross as a source of desired recombinants by a detailed study of the characteristics of a sample of plants taken from an early generation population. A large F_2 progeny of a cross of the wheat varieties Marquis and Marquillo yielded only six lines of doubtful value after five years of rigorous pedigree selection. A study of several hundred F_2 plants of this cross was thought to confirm its dubious value for the production of desirable combinations, and led Harrington to conclude that the analysis of such an early generation sample could be used as a predictive method to indicate the potential value of a cross as a source of useful segregates. Later Harrington (14), using replicated trials, found considerable differences in yield between early generation bulks of wheat crosses. The plant breeding value of these crosses was ascertained by yield trials in the F_6 to F_8 generations of lines selected for high yield from the

bulks. The results were thought to suggest that F_2 tests may be used to indicate yielding potentialities of wheat crosses.

Harlan, Martini and Stevens (12) in an extensive study which involved bulk populations of 379 barley hybrids grown for seven generations and concluded with the testing of single plant selections and composite bulks in the F_8 generation, considered that the yields of the early generation bulks prior to selection provided a good indication of the yield performances of the selections made from them. These workers thought that the results justified the procedure of eliminating the lower yielding bulks on the basis of their performance in the early segregating generations.

Immer (15), studying barley populations, came to similar conclusions and suggested that low yielding bulks could be eliminated in early generations, as they would contain fewer high yielding genotypes than the higher yielding bulks.

Subsequent investigations on this topic led to some revision of opinion of the usefulness of the method. Atkins and Murphy (3) working with hybrid oat populations, Grafius, Nelson and Dirks (11) and Peterson (30) using barley, and Fowler and Heyne (9) with winter wheat have all concluded that early generation testing is not an economical method of securing desirable segregates. On the other hand, the results of Frey (10) and Sikka, Jain and Parmar (39) had led these workers to conclude that performance of lines in early generations could be used as an indication of the value of the material as a source of valuable lines.

Tests of this nature have also been conducted quite extensively

in soybean breeding studies. Weiss, Weber and Kalton (48) found that early generation tests of bulk populations gave reasonably accurate evaluations of crosses for some characters, but were of little value in predicting yield and maturity date, while Kalton (21) in a comprehensive treatment of the problem, thought that rejection of crosses on the basis of such trials was not warranted. Mahmud and Kramer (28), on the other hand, thought good estimates of yield potential of later generation segregates from F_3 lines could be obtained if control was possible between the interaction of generations with the environment, and Voigt and Weber (47) found significantly higher yields in F_5 generation tests for the material selected by early testing compared with previously non yield-tested lines selected by standard bulk and pedigree methods. Finally Leffel and Hanson (24) in a study of early generations of a number of soybean hybrids also concluded that the performance of the parents or the crosses in early generations was a reliable predictor of the performance of lines selected from the crosses in the F_3 generation. From this review it can clearly be seen that there is considerable diversity of opinion as to the value of early generation testing for self-pollinated crops.

Studies of heritability of plant characters also have some relevance to any consideration of early testing, as these values indicate the amount of variation in a population that is genetically inherited and therefore available for exploitation by the breeder in the next generation. The yield of F_2 hybrid barley plants has been shown to contain a large fraction attributable to experimental error, while a large proportion of the genetic variance is non-heritable (11).

Heritability values established for such characters as earliness, plant height and yield are similar in several different crop plants studied. Investigations by Fiuzat and Atkins (8) in barley, Petr (31) in oats, and Johnson, Robinson and Comstock (19) as well as Bartley and Weber (4) in soybeans usually showed low heritability for yield, but higher values for such characteristics as plant height and earliness. This suggests a reason why some workers have had more success in early generation testing for the latter characters.

The principle of early testing has also found an application in corn breeding, where lines of corn are tested for combining ability early in the programme of self pollination. Early testing in corn was thought by Sprague (42) to depend on the assumptions that there are marked differences in combining ability amongst the plants selected for inbreeding, and that the selected sample based on the test for combining ability in the S_o generation provides a better sample for further inbreeding and selection than would a more random sample of the combining abilities drawn from the same population on the basis of visual selection alone. Jenkins (17), in proposing the method, published data which suggested that the ultimate combining ability of inbred lines was established very early in the process of inbreeding. Later Sprague (41) demonstrated that the yield differences in test crosses of S_o plants were sufficiently great to permit practical selection. Subsequent work (18, 25, 42) further endorsed these results, and the method found use in practical corn breeding.

The evidence in favour of the method was not accepted without criticism, however, and Richey (32, 33) in a re-examination of the early

work of Jenkins questioned the stability of combining ability and also the effectiveness of a tester to reveal segregation.

A direct outgrowth of the application of the principle of early testing to corn breeding was in the procedure of recurrent selection. It was reasoned that if the individual S_0 plants selected on the basis of test cross performance were superior as a group in combining ability to a random sample of the population, it seemed logical to intercross this group to provide the material for the next cycle of selection. This extension of early testing has been found to be an effective breeding method for increasing combining ability in both corn (27) and forage crops (20).

MATERIAL AND METHODS

A Review of Procedure

Although significant effects of chromosome substitution have already been demonstrated (22), claims for its possibilities as a plant breeding technique have been rather guarded, Kuspira and Unrau (22), for example, considered that under certain conditions its effectiveness may equal the backcross method. This attitude may be due to the fact that the results from substitution lines so far are derived from material with Chinese Spring* as the genetic background. Results of substitutions into better adapted varieties are not yet forthcoming due to the length of time required to complete a substitution programme. The procedure for chromosome substitution has been reviewed in detail by Unrau, Person and Kuspira (46) and involves the following steps:

1. Development of a chromosome deficient series in the variety into which the chromosomes are to be substituted, if one does not exist.

2. Substitution of the chromosome into the recipient variety, and reconstituting the genetic background of the latter in a more or less pure state by a series of backcrosses.

3. Selfing the monosomic progeny of the final backcross to establish the substituted chromosome in the disomic condition, preparatory to increasing the line for testing.

If only six backcrosses are made in the establishment of the new monosomic series, together with six generations of backcrossing

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* Hereafter referred to as "Chinese".

alternating with six generations of selfing in the production of the substitution, at least eighteen plant generations have elapsed before the substitution line is completed. It is for this reason that this study is devoted to early generation testing in the hope that ways of assessing the likely value of substitution combinations will be developed to ensure that the time and labour involved in the production of a substitution line is not wasted on a poor combination.

In this attempt to study the influence of a single chromosome or chromosome pair on a particular character, it is necessary to compensate for the effect of the residual genotype so that the effect of the single chromosome can be recognized. In the substitution lines this result is obtained by reconstituting the genotype of the recurrent variety for the twenty chromosome pairs not involved in the substitution. The substitution lines can then be compared directly with the recurrent variety in its pure state, and any differences between the recurrent variety and the substitution line for the characters under study can be interpreted as being due to the effect of the substituted chromosomes and their interaction with the genotype of the recurrent parent.

In this project of testing means by which desirable substitutions can be recognized in early hybrid generations, the removal of the effect of the residual genotype so that the magnitude of the effect of the chromosomes is revealed, has been attempted in two ways. The first of these methods will be known as the "F_1 Method", and involves the production of reciprocal monosomic hybrids between two varieties in which aneuploid series had been previously developed. For example:

(a) Chinese monosomic 1B ♀ x Rescue ♂

and its reciprocal

(b) Rescue monosomic 1B ♀ x Chinese ♂

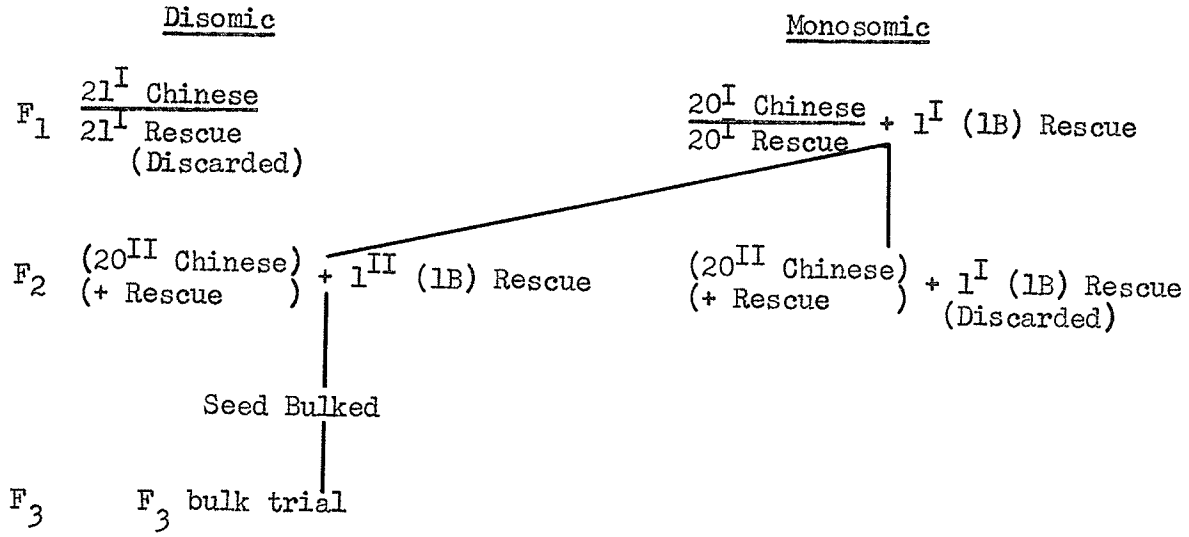
The aneuploid lines are used as the female parent in each case so as to ensure a large proportion of monosomics in the F_1 progeny. These F_1 monosomics have the following chromosomic constitution:

(a) $\frac{20^I \text{ Chinese}}{20^I \text{ Rescue}} + 1^I$ (1B) Rescue

(b) $\frac{20^I \text{ Chinese}}{20^I \text{ Rescue}} + 1^I$ (1B) Chinese

As the genetical background of these two lines are similar, differences between the (a) and (b) series of monosomic hybrids when grown in trials can be interpreted as being due to differences in potency of the two univalents with respect to the character under study.

The second method will be known as the "F_3 Bulk Method", and it shares with F_1 method the aim of minimizing differential contribution of the genetic background in the test lines to the expression of the characters studied. In this method monosomics of one wheat variety are crossed as the female parent to another wheat variety. The F_1 generation is cytologically checked, and only the monosomics retained. These are grown to maturity and from their cytologically checked progeny only the disomics are kept and grown to maturity. The seed produced by these plants is bulked to form the trial seed from which the F_3 bulk is grown. For example, Chinese monosomic 1B ♀ x Rescue♂.



This substituted F_3 bulk can be grown in field trials in comparison with an F_3 bulk population produced by the crossing of the varieties of Chinese and Rescue each in the disomic condition. In the latter bulk all the 21 chromosome pairs would be freely segregating and any differences between the two bulks could be interpreted as being due to the effect of the pair of Rescue 1B chromosomes in the substituted bulk as compared with the variety F_3 bulk in which the pair of 1B chromosomes are freely segregating. Over all the individuals in the varietal bulk and in the absence of selection the 1B chromosome pair may be thought to be composed on the average of one Rescue and one Chinese 1B chromosome.

The degree to which these differences are revealed will depend on the success obtained in equalizing the contributions of the residual genotype in the substituted bulk and in the variety hybrid bulk, and this depends on an adequate sample of the variation of the segregates in each F_2 population being obtained. To establish that any differences found between the two bulks in controlled tests are a valid estimate of the contribution made by the donated chromosomes, the parental varieties and

the substitution line involving the same varieties and for the same chromosomes can be included in the trial for the purposes of comparison.

During the course of this study, some modifications of the methods outlined were attempted, usually to reduce the amount of cytological checking that the methods involved. In the F_1 method a way of obtaining a hybrid progeny composed solely of monosomics and so eliminate the necessity of cytological checking was the use of the nullisomic deficiency rather than the monosomic for the formation of hybrids with the disomic parent. This method, however, required the use of pairs of rather vigorous and fertile nullisomic lines for its successful application.

A second modification of the F_1 method was an attempt to increase the number of plants obtained from cytologically checked lines by clonal propagation utilizing a method suggested by Professor W. J. White of the University of Saskatchewan (personal communication).

The considerable amount of cytological checking involved in the F_3 bulk method could be eliminated, if conspicuous markers for the monosomic condition in chromosome lines were available. Unfortunately only one of these, the speltoid character of monosomic 5A was well marked enough to be of use as a screening method for monosomics. The speltoid character was sufficiently distinctive, however, to be readily picked out in all cases in which this method was applied, even in segregating F_2 lines.

Selection of Chromosome Lines

As a guide to the selection of chromosome lines to be used for

the testing of the previously described methods, the work of Kuspira and Unrau (22) was consulted. There was some practical limitation imposed on the choice of lines, however, as not all the monosomic series available had a complete set of twenty one monosomics. The materials chosen for use in this project were chromosomes 1B, 3A, 4B, 6B and 7D, while line 5A was added to the list for the F_3 bulk tests because of the advantage of the speltoid character as a monosomic marker. As can readily be seen from the new chromosome notation introduced by Sears (38) the distribution of these chromosome lines amongst the genomes is:

A genome	2 lines
B genome	3 lines
D genome	1 line.

In addition each of the six lines selected belongs to a different homoeologous group. Table I lists reports in the literature of the effect of these chromosomes on the characters studied.

Selection of the Varieties Used in the Tests

As the F_3 bulk method requires substitution lines of the varieties used, with which to provide comparisons with the results of the synthesised bulks, the combination of Thatcher chromosomes substituted into Chinese was selected for the purposes of testing the method.

For the testing of the F_1 method, the prime consideration was to select a group of varieties, preferably of diverse genetical origin, in which monosomic series were already established. The varieties chosen were Chinese, Rescue, Red Bobs, Redman, and S615, (Table II).

TABLE I

REPORTS FROM LITERATURE ON THE INFLUENCE OF THE SELECTED CHROMOSOMES ON THE CHARACTERS BEING STUDIED

	Chromosome 1B	Chromosome 3A	Chromosome 4B	Chromosome 5A	Chromosome 6B	Chromosome 7D
Plant Height	Sears (37) Kuspira and Unrau (22)	Sears (37) Kuspira and Unrau (22)	Sears (37) Kuspira and Unrau (22)	Sears (37) Kuspira and Unrau (22)	Sears (37) Larson and MacDonald (23)	Sears (37) Larson and Macdonald (23)
Tillering	Sears (37)		Sears (37) Tsunewaki and Heyne (43)			
Maturity	Kuspira and Unrau (22) Allan (1)	Kuspira and Unrau (22)	Sears (37) Allan (1) Kuspira and Unrau (22)	Sears (37) Kuspira and Unrau (22)	Kuspira and Unrau (22)	Kuspira and Unrau (22)
Yield	Kuspira and Unrau (22)	Kuspira and Unrau (22)	Kuspira and Unrau (22)	Kuspira and Unrau (22)	Kuspira and Unrau (22)	Kuspira and Unrau (22)
Kernel Weight	Kuspira and Unrau (22)				Kuspira and Unrau (22)	

TABLE II

PARENTAGE OR ORIGIN OF THE VARIETIES USED IN THE STUDY

Variety	Parentage or Origin
Chinese	Introduction, presumably originally from China
Thatcher	(Iumillo x Marquis) x (Kanred x Marquis)
Rescue	Apex x S615
Red Bobs	Selection from Early Triumph
Redman	Regent x Canus
S615	Introduction, originally from Portugal

Selection of Plant Characteristics

As the intention of this study is to explore the application of the substitution method to plant breeding, the characters of the wheat plant investigated are all of a quantitative nature, and important in wheat breeding programmes. A quantitative character is thought to be one which does not segregate into discontinuous categories in the segregating generations. It is thought to be determined by a number of genes, in some cases only a few, in others the numbers may be considerable. Grain yield, for example, could well involve the entire gene complement as yield may be thought of as an expression of the harmonious operation of all genes of the plant. Of the other characters studied, plant height and earliness are probably governed by a small number of genes, but the inheritance of tillering and kernel weight, both of which

are components of yield, is probably more complex.

Cytological Techniques

Pollen Mother Cell Analysis. Plants of monosomic lines growing in the field that were intended to be used for crossing were cytologically checked by pollen mother cell analysis and all but the plants with 20^{II} and 1^{I} configurations were discarded. The acetocarmine squash technique as described by Smith (40) was employed, using Carnoy's A fluid as the fixitive. Plants that were identified as being monosomic by this method were distinctively labelled in the field.

Root-Tip Analysis. In screening populations of seedlings for monosomics or disomics as required by the methods being tested, the Feulgen squash method of root-tip analysis was utilized. The details of the method were as outlined in a study of Tsunewaki and Heyne (44). This procedure was found by Tsunewaki and Jenkins (45) to be the most efficient in dealing with aneuploid populations. The technique was the standard procedure followed in the laboratory in which the study was conducted, and involved a twenty four hour period of cold pre-treatment of the root-tips, followed by fixation in Farmer's fluid.

In the cytological records for the mitotic studies each seedling sampled was given a consecutive number which identified the root-tip material through to cytological examination, and also the plant to which the root-tip sample belonged if it was selected and grown to maturity. This method was found to be an efficient and reliable way of dealing with the large numbers of somatic chromosome checks that the experimental methods involved.

Production and Testing of the Experimental Materials

The methods used in this study, as previously outlined, required a considerable number of hybrid combinations of wheat lines, both monosomic and disomic, to be made. Table III lists the number of crosses made in the different sections of the project.

F_1 Method: To test this method, the original intention was to grow the test material in replicated tests of spaced plants, using five chromosome lines, each line forming a separate trial and each trial being replicated ten times and involving five varieties. Material involving the deficiency of chromosome 5A was not used due to the restriction imposed on yielding capacity by the speltoid character of the monosomics.

Unfortunately, due to shortage of hybrid seed, or lack of monosomics in some of the chromosome lines, not all the trials could be sown with the full complement of five varieties. In order to have in the trial, material available for all possible comparisons that could prove useful in the evaluation of the method, a full range of monosomic and disomic lines of the parental varieties and their hybrids was included in the tests.

The list below gives the number and types of lines used in the trials.

	Number of varieties in the trial	
	5	4
Disomic Parents	5 lines	4 lines
Monosomic Parents	5 lines	4 lines
Disomic Hybrids	20 lines	12 lines
Monosomic Hybrids	20 lines	12 lines
Total	50 lines	32 lines

TABLE III

TYPES AND NUMBERS OF CROSSES MADE FOR THE PRODUCTION OF HYBRID MATERIAL TO TEST THE "F_1" AND "F_3" METHODS

Hybrid Groups	Time and Place	Field 1959	Greenhouse 1959-60	Field 1960	Greenhouse 1960-61	Totals
F_1 method	Chinese monosomics x varieties	21	55		5	81
	Rescue monosomics x varieties	18	48		7	73
	Red Bobs monosomics x varieties	28	40		9	77
	Redman monosomics x varieties	30	41		7	78
	S615 monosomics x varieties	14	30		6	50
	Variety hybrids	34	17	26	44	121
	Nullisomics x disomics				41	41
F_3 method	Chinese monosomics x Thatcher	46				46
	Chinese x Thatcher	4	1			5
	Rescue 5A monosomics x varieties			14		14
	Rescue x varieties			8		8
	Totals	195	232	48	119	594

As a consequence spaced trials consisted of fifty or thirty-two genetically different lines in each replication, depending on whether five or four varieties were included. Each line was represented by only a single plant in a replication.

The following spaced-plant trials were planted in the two seasons in which tests were made.

	Chromosome Number	Varieties	Replications
1960			
	1B	Chinese, Rescue, Red Bobs, Redman	10
	3A	Chinese, Rescue, Red Bobs, Redman, S615	10
	4B	Chinese, Rescue, Red Bobs, S615	8
	7D	Chinese, Rescue, Red Bobs, Redman	8
1961			
	6B	Chinese, Rescue, Red Bobs, Redman, S615	12

In 1960 the seedlings used in these trials were grown in $2\frac{1}{2}$ inch earthenware pots, each identified by its consecutive number or code letters. In 1961 the seedlings were planted out in 2-inch "jiffy pots", a change which facilitated handling and planting of the test material. In all cases the plants requiring cytological examination were sampled prior to being potted.

Modifications of the F_1 Method. In an attempt to obtain for trial purposes monosomic seed that did not require cytological checking, the crossing of nullisomics to disomics was resorted to. The material used to test this method depended on the availability of a pair of reasonably fertile nullisomic lines in different varieties but deficient

for the same chromosome pair. Such a pair was found in Redman and Rescue nullisomic 7D. It seemed that nullisomics were found with rather high frequency in the progenies of the selfed monosomics of these lines.

The following hybrid combinations were made in the greenhouse during the winter of 1960:-

Redman nullisomic 7D x Rescue

Rescue " 7D x Redman

Redman " 7D x Redman

Rescue " 7D x Rescue

The crosses were made using the nullisomic as either the male or the female parent, and while the seed set was low in both cases, the second combination seemed to be rather more successful. A small replicated spaced plant trial of the above material together with the parental varieties and reciprocal disomic hybrids was planted late in the spring of 1961.

The possibility of increasing the number of plants obtained for testing from a cytologically checked plant was explored by the application of a method of clonal propagation of wheat plants used by Professor W. J. White.

The cytologically checked seedlings were planted in large plastic pots of vermiculite and watered from time to time with Knop's solution as a source of mineral nutrients. The plants were kept in a growth cabinet at about 60°F. for a period of about thirty days by which time they had tillered out freely. The plants were removed from the pots, and the roots shaken free of vermiculite. The crown was then divided up by a sharp scalpel into three portions, each bearing

normally two tillers and one or more crown roots. The plant segments were then potted up in soil, in large size ($4\frac{1}{2}$ inch) jiffy pots, well watered and placed in a rather cool growth cabinet for about a week to allow the root system to re-establish.

The materialsused to test this method were reciprocal Chinese x Redman chromosome 1B hybrids, their monosomic and disomic parents and the reciprocal disomic hybrids. Three clonally produced plants obtained from each line provided three replications of a spaced trial planted out in the summer of 1961.

Measurement of the Plant Characteristics under Investigation.

The pot labels in the field were checked against the sowing plan to ensure that no errors in planting had occurred. At maturity the spaced plants were pulled, labelled with a tag bearing the chromosome line, replication number and the line number of the plant and stored in sheaves until the remaining measurements could be made.

1. The heading date was taken when the first head had completely cleared the sheath of the flag-leaf.

2. Plant height was measured from the level of the crown to the tips of the main heads, excluding the awns where these were present. On the basis of this measurement the plant was placed in one of a series of three-inch size classes with respect to its height.

3. The tiller number was counted on the harvested plants, with a distinction being made between main and late tillers.

4. Total yield of the plant was taken from the grain threshed with a single plant threshing machine, the blower of which was cut down so that small or shrivelled grains were not cleaned out.

The F_3 Bulk Method. The work for this section of the study was initiated in the summer of 1959 when crosses between the chosen Chinese monosomic lines and Thatcher and between the varieties Chinese and Thatcher were made. The F_1 seedlings of each of the Chinese monosomic x Thatcher hybrids were checked cytologically by root-tip analysis, and about ten monosomics in each line grown through to maturity. The F_2 seeds obtained from these plants were also cytologically checked and only the disomics retained. Owing to the large number of plants involved at this stage of the programme, these were planted out in greenhouse beds.

The original intention was to have about a hundred disomic F_2 plants contributing to each F_3 bulk, so as to have a good sample of the variability of the F_2 of the cross represented in the bulk. This number proved to be too ambitious considering the time and assistance available, and the final aim was modified to have at least fifty F_2 plants in each bulk population. Table IV lists the number of disomic plants in each F_3 bulk. The Chinese x Thatcher variety hybrids were treated similarly except that cytological examination was not necessary. A small F_1 population, and a sufficiently large F_2 to provide at least fifty plants for the bulks were grown. The Chinese 5A x Thatcher hybrids were similarly dealt with, but a larger F_2 population was grown from the speltoid (and therefore monosomic) F_1 plants so that sufficient square headed disomics could be obtained for the F_3 bulks. To test if a sample of about fifty F_2 plants was sufficient to give a reliable assessment of the characteristics of the cross, two chromosome 5A F_3 bulks and two F_3 varietal hybrid bulks were made to test the consistency of their performance.

TABLE IV

NUMBER OF DISOMIC PLANTS COMBINED IN THE F_3 BULKS OF CHINESE x THATCHER HYBRIDS

Hybrid Combination	Number of plants in bulk
Chinese 1B x Thatcher	43
Chinese 3A x Thatcher	48
Chinese 4B x Thatcher	64
Chinese 5A x Thatcher (A)	69
Chinese 5A x Thatcher (B)	68
Chinese 6B x Thatcher	65
Chinese 7D x Thatcher	78
Chinese x Thatcher (A)	50
Chinese x Thatcher (B)	40

To make up the F_3 bulk, the seed from two heads of each disomic F_2 plant was combined. This was to ensure a more or less equal contribution of each plant to the bulk population. Only grain grown in the greenhouse during the winter of 1959-60 was used in seeding the trial, to ensure that all the seed was produced under comparable conditions. For this reason, as well as to increase the amount of seed and check its purity the parental varieties and substitution lines were also grown in the greenhouse beds at this time.

As the majority of the materials involved in seeding of the trial was harvested shortly before the sowing date, it was thought to be necessary to give the grain a period of cold treatment to break its

dormancy, and ensure immediate germination. For this reason all the seed to be down in the field trial was subjected to a twenty four hour period of soaking in water at ±0°C., followed by a further five days storage period at this temperature. That this method was effective in breaking any dormancy was shown by Petri dish germination tests, and was reflected by even field germination.

This rather full winter programme precluded the completion of all the F_3 bulks in time for sowing in the spring of 1960. The field trial was sown with a total of fourteen lines made up as follows:- two parental varieties; six substitution lines: 1B, 3A, 4B, 5A, 6B, 7D; four F_3 substituted bulks: 5A (two), 3A and 6B; and two F_3 variety hybrid bulks.

These lines were planted with a V-belt seeder in a six replication randomized block design, each plot consisting of two 10-foot rows, one foot apart, and each plot separated by a row of Kharkov winter wheat. The sowing rate was one gm. per foot of row. The trial was sown on the 24th of May and harvested as the plots reached maturity, the harvesting being completed by the end of August.

As the whole series of substituted bulks was not ready for testing in the field by late May of 1959, a greenhouse trial, utilizing two greenhouse beds was designed for the early spring of 1960. Fifteen lines were tested in this trial, a randomized block layout with six replications. They were the two parental varieties, Chinese and Thatcher; six substitution lines, 1B, 3A, 4B, 5A, 6B, 7D; six substituted F_3 bulks involving the same chromosomes as the substitutions, and one F_3 hybrid bulk between the two parental varieties. Each plot was a

single row, four feet long, and spaced six inches apart. A sowing rate of 3/4 gm. per foot of row was adopted to ensure a good stand of plants. The trial was sown on the 18th of April, rather later than had been planned.

In the summer of 1961 an F_4 trial of the material that had been grown in the F_3 trial of the previous year was sown. As the amount of seed available was not the limiting factor of plot size, a five replication rod-row randomized block layout was designed. The two row plot with one foot between rows and separated by a row of Kharkov winter wheat and the sowing rate of one gm. per foot of row plan was maintained in this trial to allow comparisons to be made with the previous year's results. The trial was machine sown on the 15th of May, 1961.

Finally the surplus seed of the F_3 bulks hitherto not tested in the field was sown out as observation plots, with two 9-foot rows per plot and at a sowing rate of one gm. per foot of row. The parental varieties and appropriate substitution lines were included for comparisons, and the area sown with the V-belt seeder in the spring of 1961.

Modification of the F_3 Bulk Method. The manner in which the monosomic marker on chromosome 5A can be used has already been illustrated in the Chinese monosomic x Thatcher F_3 trials. In an attempt to test this method more exhaustively, crosses were made to Rescue 5A and also Rescue itself by eight different varieties used as male parents. Of the eight varieties used in this trial, Chinese, Red Bobs, Redman, S615 and Thatcher have already been discussed, while Pembina, the new Canadian variety, and two New Zealand varieties, Aotea and Hilgendorf, were added.

The F_1 generation of these lines was grown in the greenhouse in

pots, and in the case of the monosomic lines only the speltoids were used to give rise to the F_2 progeny. This generation was grown in the greenhouse beds, with only the normal headed (non-speltoid) types being collected to form the F_3 bulk which was handled as has been described before. Both of these generations were grown in the winter of 1960-61.

The F_3 bulk grain was cold treated before sowing to break dormancy, but due to the low frequency of disomics only sufficient grain was obtained to sow two sets of observation plots, each plot of two rows, each row nine feet long and spaced one foot apart with the sowing rate of one gm. per foot of row. This shortage of seed caused the hybrid combination involving Hilgendorf to be removed altogether. Table V lists the number of disomics involved in each chromosome 5A bulk population. The lines sown in these plots were seven Rescue 5A x variety F_3 bulks, seven Rescue x variety F_3 bulks, and the variety Rescue itself. The measurements and observations were taken in the same manner already described for the F_3 bulks.

Measurement of the Plant Characteristics under Investigation in the F_3 Bulk Method.

1. Heading date was recorded when it was judged that half the heads of the plot were clear of the sheath of the flag-leaf.

2. Plant height was taken as the average of the whole plot, the lines being classed in three-inch height groups with respect to this character. The genetic heterogeneity of some of the test material made the estimation of this character and also the heading date, rather difficult.

3. For plot yield, the whole plot was cut, and the sheaves

TABLE V

NUMBER OF DISOMIC PLANTS INVOLVED IN THE RESCUE 5A F_3 HYBRID BULKS

Hybrid Combination	Number of plants in the bulk
Rescue 5A x Chinese	22
Rescue 5A x S615	21
Rescue 5A x Aotea	23
Rescue 5A x Hilgendorf	15
Rescue 5A x Red Bobs	18
Rescue 5A x Redman	26
Rescue 5A x Pembina	24
Rescue 5A x Thatcher	27

threshed with a threshing mill, or in the case of the smaller greenhouse plots, on the single plant thresher.

4. Kernel weight determinations were made on samples of grain, two lots each of a hundred grains for each line being counted and weighed.

Statistical Treatment of the Results

For the F_1 trials an analysis of variance was applied to the randomized block design, with three groups of lines being analysed separately. These were the parental monosomics and disomics, the disomic hybrids, and the monosomic hybrids. Duncan's multiple-range test was applied to the means to determine the significant differences.

The F_3 trials were treated in a similar manner, the randomized

block layout was analysed, and the significance of the differences determined by Duncan's test.

Review of the Seasons in which the Trials were Grown

1960:

In a favorable season for plant growth, the trials grew vigorously, but in the spring considerable weeding was necessary to rid the test area of volunteer rape plants from the previous season's crop. Little damage from cutworms was observed, but the transplants in the spaced trial were sprayed with Deildrin at one ounce per gallon at the time of planting to protect them from attack. Due to their favourable location between two winter wheat areas, the trials were almost untouched by birds prior to harvest, but some slight bird damage occurred in the stored sheaves before they were threshed. An early attack of wheat stem rust, induced artificially in nearby plots was a serious problem, but spraying with nickel chloride and Dithane in a mixture at a concentration of 15 gm. of each in three gallons of water, applied with a knapsack sprayer at seven to ten-day intervals helped to minimize the effects of the disease.

1961:

In this season the trials were grown in an area of land remote from trees, but of a rather exposed aspect. During the very dry growing season, two applications of irrigation water, by overhead sprinklers early in June and early in July were thought to be necessary. Stem rust made only a late appearance in this season and did little damage. No attempt was made to control it. However, large flocks of sparrows appearing in early August at the time of the filling of the grain so

devastated the trials that no yield figures could be obtained. Attempts to control the birds proved to be ineffective.

Chronology of the Work

Table VI summarizes the progress of the work during the course of the study.

TABLE VI

CHRONOLOGY OF THE WORK

Season and Year	Nature of the Work
Summer 1959	1. Monosomics of the varieties Chinese, Rescue, Red Bobs, Redman and S615 were grown. 2. Crossing of selected lines for F_1 method was started. 3. Chinese monosomics of selected lines were crossed by Thatcher for the production of the F_3 bulks.
September to December 1959	1. Monosomics of F_1 Chinese monosomics x Thatcher were grown out.
January to April 1960	1. Crossing of selected lines for F_1 trial was continued. 2. Disomics of F_2 Chinese x Thatcher cross were grown out. 3. Chinese, Thatcher, and appropriate substitution lines were grown for seed increase and as a check for purity.

Season and Year	Nature of the Work
Summer 1960	1. Chinese x Thatcher F_3 bulk trial was grown. 2. F_1 spaced trials for chromosomes 1B, 3A, 4B, and 7D were grown. 3. Further crosses for F_1 method were made. 4. Crosses of Rescue and Rescue 5A x eight varieties were made for F_3 bulk test.
Winter 1960-61	1. Chinese x Thatcher F_3 bulk trial was grown in greenhouse beds. 2. Further crosses for F_1 method trials were made. 3. Rescue and Rescue 5A F_3 hybrid bulks were established by growing F_1 and F_2 generations. 4. Reciprocal crossing of Redman and Rescue 7D nullisomics x disomics was started. 5. The material for clonal propagation test was grown.
Summer 1961	1. Chinese x Thatcher F_4 bulk trial was sown. 2. F_1 spaced trial chromosome 6B was planted. 3. Observation plots of Rescue 5A F_3 bulks were sown. 4. Observation plots of Chinese x Thatcher F_3 bulks were sown. 5. Trial of Rescue, Redman 7D nullisomic x disomic crosses was planted. 6. Clonal material of F_1 Chinese x Redman 1B hybrids was grown in trial.

RESULTS

Cytology

In the course of this study, a large number of cytological determinations, particularly of somatic mitosis, was made. As the majority of the materials checked was the progeny of selfed monosomics, or monosomic x disomic hybrids, the results may be taken as an indication of the relative frequency at which monosomics are produced in these lines, with respect to both the chromosome and the variety involved. The data listed in Table VII were obtained from root tip analysis of the materials used in the F_1 method. These results seem to indicate that the varieties Red Bobs and Redman tended to give higher proportion of monosomics in progenies, both of selfed monosomics and monosomic hybrid combinations, than the other varieties used in the study. On the other hand the selfed monosomics of the variety S615 appeared to give a low yield of monosomics. In a consideration of the behaviour of the individual chromosomes in all the combinations tested (Table VIII), it seemed that plants monosomic for chromosome 7D produced fewer monosomics in their progenies than did other chromosome lines. On the other hand, this line produced a higher frequency of nullisomics, a result that does not agree very well with Sears' work (37) based on the variety Chinese.

The cytological results derived from F_1 and F_2 generations of the F_3 bulks (Table IX) did not indicate any great difference in behaviour between the different chromosome lines. It was notable that the percentage of monosomics for the F_1 generation was higher than that of the F_2.

TABLE VII

FREQUENCY OF MONOSOMICS IN THE VARIETAL AND HYBRID MONOSOMICS STUDIED IN THE F_1 METHOD

Variety involved, or female monosomic parent in hybrid combination	Chromosome	Variety: Total Plants checked	Variety: % Monosomic	Variety: Reported % Monosomic (44)	Hybrid Combinations: Total Plants checked	Hybrid Combinations: % Monosomic
Chinese	1B	32	56.3	73.1	66	60.6
	3A	39	76.9	80.0	72	66.7
	4B	28	67.9	71.4	59	59.3
	6B	36	58.3	56.9	74	63.5
	7D	25	44.0	72.9	55	61.8
	Total	160	61.9		326	62.6
Rescue	1B	30	76.7		35	62.9
	3A	22	63.6		50	84.0
	4B	23	78.3		55	70.9
	6B	41	58.5		72	69.4
	7D	31	61.3		43	51.2
	Total	147	66.7		255	68.6
Red Bobs	1B	24	79.2		31	74.2
	3A	29	72.4		44	72.7
	4B	25	84.0		40	65.0
	6B	19	89.5		81	81.5
	7D	23	43.5		33	84.9
	Total	120	73.3		229	76.4
Redman	1B	29	82.8		46	80.4
	3A	27	70.4		72	61.1
	4B	20	80.0		27	70.4
	6B	34	61.8		77	79.2
	7D	18	72.2		45	80.0
	Total	128	72.7		267	73.8
S615	1B	6	33.3		-	-
	3A	22	63.6		47	85.1
	4B	28	53.6		44	65.9
	6B	41	58.5		60	75.0
	7D	11	36.4		30	36.7
	Total	108	54.6		181	69.1

TABLE VIII

FREQUENCY OF MONOSOMICS IN THE CHROMOSOME LINES STUDIED IN THE F_1 METHOD

Chromosome Number	Varieties			Hybrids		Total	
	Total	% Monosomics	% Nullisomics	Total	% Monosomics	Total	% Monosomics
1B	121	71.1	1.7	178	68.5	299	69.6
3A	139	70.5	5.4	285	72.3	424	71.7
4B	124	71.7	0.8	225	65.8	349	67.9
6B	171	62.6	1.2	364	73.9	535	70.3
7D	108	52.8	10.2	206	63.6	314	59.9
Total	663	65.9	3.5	1258	69.6	1921	68.4

TABLE IX

FREQUENCY OF MONOSOMICS IN THE CHINESE x THATCHER BULKS USED IN THE F_3 METHOD

Hybrid combination	F_1 Generation		F_2 Generation	
	Total	% Monosomics	Total	% Monosomics
Chinese 1B x Thatcher	14	71.4	194	64.5
Chinese 3A x Thatcher	19	73.7	362	61.7
Chinese 4B x Thatcher	22	68.2	190	64.5
Chinese 6B x Thatcher	17	70.6	325	67.5
Chinese 7D x Thatcher	20	75.0	309	61.3
Total	92	71.7	1380	63.7

Another measure of the proportion of monosomics was obtained by studying the number of speltoids in progenies of monosomics involving chromosome 5A. The results from this type of material, both from the Chinese x Thatcher lines and the Rescue hybrids, are listed in Table X.

The overall higher monosomic percentage in this chromosome 5A material, as compared with the other chromosome lines studied, indicates a higher incidence of loss of the univalent in gametogenesis, this being particularly so in the Rescue hybrids. As in Table IX a higher proportion of monosomics was found in the F_1 generation than in the F_2.

TABLE X

FREQUENCY OF MONOSOMICS IN THE CHROMOSOME 5A HYBRID COMBINATIONS TESTED BY THE F_3 METHOD

Hybrid combination	F_1 Generation		F_2 Generation	
	Total	% Monosomics	Total	% Monosomics
Rescue 5A x Chinese	18	94.4	109	79.8
" x S615	17	82.4	110	80.9
" x Aotea	19	94.7	97	76.3
" x Hilgendorf	21	90.5	84	82.1
" x Red Bobs	17	94.1	112	83.9
" x Redman	13	84.6	115	79.1
" x Pembina	17	82.4	115	79.1
" x Thatcher	12	83.3	113	76.1
Total	134	88.8	857	79.5
Chinese 5A x Thatcher	No data		589	72.5

The F_1 Method

From the five trials planted for the purpose of testing this method, the characters of yield of grain and days to heading were selected for analysis. Results for yield were available from two trials, the others being damaged by rust or by birds to the extent where their results could not be relied upon. The figures on days to heading were, on the

other hand, available from all five trials. Within the individual trials, some replications also suffered losses, due to the planting of incorrect material, death of plants or accidental damage. If only one or two plants in a replication were involved, missing plot values were calculated for them. If the damage was more extensive than this, the replication was discarded. The chromosome lines in which the characters were studied, together with the number of acceptable replications available, are listed below.

Grain Yield

Chromosome	1B	8 Replications
"	3A	7 "

Days to Head

Chromosome	1B	8 Replications
"	3A	7 "
"	4B	7 "
"	6B	12 "
"	7D	6 "

For the purposes of analysis each trial grown to test this method was divided into three separate sections.

1. The parental monosomics and disomics were analysed as a block to determine if the absence of a particular chromosome had a significant effect on the expression of the character studied.

2. The disomic hybrids were analysed as a group to determine if differences could be detected between reciprocal hybrids. For each of the characters studied an example of this analysis is presented.

3. The monosomic hybrids were analysed as a group to determine if the univalent chromosomes differed in their contribution to the character investigated.

Grain Yield: Chromosome 1B. The results for grain yield evaluations of this trial are presented in Tables XI to XIII.

The absence of significant interaction between the disomic varieties and their monosomics indicates that the varieties tested tend to react in similar fashion to the absence of chromosome 1B, all of them showing a reduction in yield. A significant difference between the disomics collectively and their monosomics, indicates that chromosome 1B has important effects as far as yield is concerned, (Table XI).

The analysis of the disomic hybrids indicates that the hybrids of the reciprocal pairs did not differ significantly in yield, (Table XII).

Comparisons of the reciprocal monosomic pairs indicate quite large and significant differences between pairs of lines differing only in the source of the chromosome present in the monosomic condition, (Table XIII). The grouping of varieties with respect to their significant yield differences shows that Redman 1B is appreciably superior to the other 1B chromosomes tested in its influence for the increase of yield.

Grain Yield: Chromosome 3A. (Tables XIV and XV). From the analysis of the varietal monosomics and disomics, chromosome 3A does not appear to be very important as far as yield is concerned, the yield of the monosomics being only slightly less than that of the disomics, and all the varieties acting similarly, (Table XIV).

Some important differences are revealed in the monosomic hybrids however, chromosome 3A of S615 seeming to be markedly poorer than in most of the other varieties. These latter seem to react in a similar fashion to each other, though Red Bobs 3A seems to be superior to Chinese 3A, (Table XV).

TABLE XI

THE EFFECT OF THE ABSENCE OF CHROMOSOME 1B ON THE YIELD OF FOUR WHEAT VARIETIES

Disomic	Mean yield in gm.	Monosomic		Mean yield in gm.
Chinese	50.0	Chinese	1B	41.9
Rescue	39.6	Rescue	1B	17.6
Red Bobs	28.3	Red Bobs	1B	21.9
Redman	32.7	Redman	1B	16.1
Mean	37.7		Mean	24.4

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	7	1956	279	3.07**
Varieties	3	4920	1640	18.02**
Disomics V. Monosomics	1	2828	2828	31.08**
Disomics X Monosomics	3	648	216	2.37
Error	48	4370	91	
Total	62	14722		

Least Significant Difference at 5% level: 9.4
" " " " 1% " : 12.6

NS denotes non significant
* " significant at 5% level
** " " " 1% "
In this and subsequent tables, the symbol NS denotes non significant.

TABLE XII

THE YIELD OF RECIPROCAL F_1 WHEAT VARIETY HYBRIDS

Hybrid Combination		Mean yield in gm.	Significance of difference
Chinese	x Rescue	87.9	NS
Rescue	x Chinese	77.4	
Chinese	x Red Bobs	47.3	NS
Red Bobs	x Chinese	54.7	
Chinese	x Redman	54.9	NS
Redman	x Chinese	44.9	
Rescue	x Red Bobs	45.2	NS
Red Bobs	x Rescue	32.6	
Rescue	x Redman	40.3	NS
Redman	x Rescue	41.5	
Red Bobs	x Redman	36.9	NS
Redman	x Red Bobs	36.3	

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	7	1,598	228.3	1.72
Hybrids	11	25,253	2295.7	17.31**
Error	75	9,946	132.6	
Total	93	36,797		

L.S.D. on Duncan's Multiple-Range Test.
at 5% level: 11.6 to 13.8
" 1% " : 15.4 to 18.0

TABLE XIII

THE COMPARISON OF THE YIELD OF RECIPROCAL F_1 MONOSOMIC X DISOMIC HYBRIDS INVOLVING CHROMOSOME 1B

Hybrid Combination	Chromosome as Univalent	Mean yield in gm.	Significance of difference
Chinese 1B x Rescue	Rescue 1B	59.3	N.S.
Rescue 1B x Chinese	Chinese 1B	52.2	
Chinese 1B x Red Bobs	Red Bobs 1B	19.6	*
Red Bobs 1B x Chinese	Chinese 1B	31.1	
Chinese 1B x Redman	Redman 1B	36.3	**
Redman 1B x Chinese	Chinese 1B	21.8	
Rescue 1B x Red Bobs	Red Bobs 1B	20.3	N.S.
Red Bobs 1B x Rescue	Rescue 1B	28.6	
Rescue 1B x Redman	Redman 1B	30.8	*
Redman 1B x Rescue	Rescue 1B	22.4	
Red Bobs 1B x Redman	Redman 1B	43.3	**
Redman 1B x Red Bobs	Red Bobs 1B	18.3	

Significant effects at 1% level: Redman > Chinese, Red Bobs

at 5% level: Redman > Rescue

Chinese > Red Bobs

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	7	273	39	0.46
Lines	11	15,894	1,445	17.20**
Error	77	6,468	84	
Total	95	22,635		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 9.0 to 10.8
" 1% " : 11.9 to 14.0

TABLE XIV

THE EFFECT OF THE ABSENCE OF CHROMOSOME 3A ON THE YIELD OF FIVE WHEAT VARIETIES

Disomic	Mean yield in gm.	Monosomic		Mean yield in gm.
Chinese	24.0	Chinese	3A	23.0
Rescue	31.0	Rescue	3A	21.7
Red Bobs	14.9	Red Bobs	3A	11.2
Redman	16.9	Redman	3A	10.2
S615	34.3	S615	3A	31.2
Mean	24.2		Mean	19.4

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	6	207	34.5	3.15*
Varieties	4	3,912	978.1	89.32**
Disomics v. Monosomics	1	384	383.8	3.51
Disomics x Monosomics	4	213	53.3	0.49
Error	51	5,585	109.5	
Total	65	10,301		

L.S.D. at 5% level: 11.3
" " 1% " : 15.0

TABLE XV

THE COMPARISON OF THE YIELD OF RECIPROCAL F_1 MONOSOMIC x DISOMIC HYBRIDS INVOLVING CHROMOSOME 3A

Hybrid Combination		Chromosome as Univalent		Mean yield in gm.	Significance of Difference
Chinese 3A	x Rescue	Rescue	3A	41.8	N.S.
Rescue 3A	x Chinese	Chinese	3A	34.7	
Chinese 3A	x Red Bobs	Red Bobs	3A	17.7	*
Red Bobs 3A	x Chinese	Chinese	3A	8.1	
Chinese 3A	x Redman	Redman	3A	13.0	N.S.
Redman 3A	x Chinese	Chinese	3A	17.9	
Chinese 3A	x S615	S615	3A	9.7	N.S.
S615 3A	x Chinese	Chinese	3A	14.0	
Rescue 3A	x Red Bobs	Red Bobs	3A	17.8	N.S.
Red Bobs 3A	x Rescue	Rescue	3A	15.8	
Rescue 3A	x Redman	Redman	3A	16.5	N.S.
Redman 3A	x Rescue	Rescue	3A	19.2	
Rescue 3A	x S615	S615	3A	22.7	**
S615 3A	x Rescue	Rescue	3A	40.1	
Red Bobs 3A	x Redman	Redman	3A	15.9	N.S.
Redman 3A	x Red Bobs	Red Bobs	3A	17.2	
Red Bobs 3A	x S615	S615	3A	13.5	**
S615 3A	x Red Bobs	Red Bobs	3A	25.9	
Redman 3A	x S615	S615	3A	16.9	**
S615 3A	x Redman	Redman	3A	31.2	

Significant effects at 1% level: Rescue, Red Bobs, Redman > S615

at 5% level: Red Bobs > Chinese

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	6	213	35.5	0.73
Lines	19	11,980	630.5	12.95**
Error	109	5,304	48.7	
Total	134	17,497		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 7.4 to 9.2
" 1% " : 9.8 to 11.8

Days to Heading: Chromosome 1B (Tables XVI to XVIII) All the varieties tested react in a similar manner to the lack of chromosome 1B, with respect to heading date; the monosomics being collectively rather later than the disomics. Marked varietal differences were revealed for this character however both for the monosomic and disomic states, (Table XVI).

The results shown in Table XVII demonstrate that the pairs of hybrids in the reciprocal crosses of the disomics do not differ in heading date.

In the monosomic hybrid comparisons, only a single significant difference was revealed, that of Chinese 1B over Redman, (Table XVIII).

Days to Heading: Chromosome 3A (Tables XIX and XX) No differential action of the varieties tested with respect to the loss of chromosome 3A on heading date was revealed by the test, though the varieties differed substantially in this character, (Table XIX).

The monosomic hybrids by comparison revealed some marked differences, with 3A of S615 inducing later heading than 3A of Rescue and Red Bobs, while Chinese 3A was later than Red Bobs, (Table XX).

Days to Heading: Chromosome 4B (Tables XXI and XXII) The absence of chromosome 4B did not apparently influence the heading time of the varieties tested taken as a group, but the highly significant interaction between the parental varieties and their monosomics indicates a differential response of the varieties in heading date to the absence of chromosome 4B, (Table XXI).

Although significant differences are revealed in the monosomic hybrids, there is a lack of consistent behaviour in some varieties par-

TABLE XVI

THE EFFECT OF THE ABSENCE OF CHROMOSOME 1B ON THE NUMBER OF DAYS TO HEADING OF FOUR WHEAT VARIETIES

Disomic	Mean days to Head	Monosomic		Mean days to Head
Chinese	55.6	Chinese	1B	55.6
Rescue	47.0	Rescue	1B	47.1
Red Bobs	40.5	Red Bobs	1B	42.5
Redman	40.9	Redman	1B	43.0
Mean	46.0		Mean	47.1

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	7	4	0.6	0.15
Varieties	3	2,070	690.0	172.50**
Disomics v. Monosomics	1	18	18.0	4.50*
Disomics x Monosomics	3	16	5.3	1.32
Error	48	192	4.0	
Total	62	2,300		

L.S.D. at 5% level: 2.0
" " 1% " : 2.7

TABLE XVII

THE NUMBER OF DAYS TO HEADING OF RECIPROCAL F_1 WHEAT VARIETY HYBRIDS

Hybrid Combination		Mean days to head	Significance of Difference
Chinese	x Rescue	47.6	N.S.
Rescue	x Chinese	48.5	
Chinese	x Red Bobs	45.1	N.S.
Red Bobs	x Chinese	45.0	
Chinese	x Redman	44.6	N.S.
Redman	x Chinese	44.6	
Rescue	x Red Bobs	40.8	N.S.
Red Bobs	x Rescue	42.6	
Rescue	x Redman	41.0	N.S.
Redman	x Rescue	42.5	
Red Bobs	x Redman	41.9	N.S.
Redman	x Red Bobs	43.1	

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	7	39	5.57	1.25
Hybrids	11	523	47.55	10.69**
Error	77	343	4.45	
Total	95	905		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 2.1 to 2.5
" 1% " : 2.8 to 3.3

TABLE XVIII

THE COMPARISON OF THE NUMBER OF DAYS TO HEADING OF RECIPROCAL F_1 MONOSOMIC x DISOMIC HYBRIDS INVOLVING CHROMOSOME 1B

Hybrid Combination		Chromosome as Univalent		Mean days to Head	Significance of difference
Chinese 1B	x Rescue	Rescue	1B	50.1	N.S.
Rescue 1B	x Chinese	Chinese	1B	49.3	
Chinese 1B	x Red Bobs	Red Bobs	1B	45.6	N.S.
Red Bobs 1B	x Chinese	Chinese	1B	45.0	
Chinese 1B	x Redman	Redman	1B	44.0	**
Redman 1B	x Chinese	Chinese	1B	46.3	
Rescue 1B	x Red Bobs	Red Bobs	1B	42.5	N.S.
Red Bobs 1B	x Rescue	Rescue	1B	42.8	
Rescue 1B	x Redman	Redman	1B	44.6	N.S.
Redman 1B	x Rescue	Rescue	1B	43.1	
Red Bobs 1B	x Redman	Redman	1B	41.6	N.S.
Redman 1B	x Red Bobs	Red Bobs	1B	41.9	

Significant effects at 1% level: Chinese > Redman

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	7	13	1.9	0.79
Lines	11	660	60.0	25.00**
Error	77	186	2.4	
Total	95	859		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 1.6 to 1.8
" 1% " : 1.5 to 2.4

TABLE XIX

THE EFFECT OF THE ABSENCE OF CHROMOSOME 3A ON THE NUMBER OF DAYS TO HEADING OF FIVE WHEAT VARIETIES

Disomic	Mean days to Head	Monosomic		Mean days to Head
Chinese	55.7	Chinese	3A	52.9
Rescue	44.9	Rescue	3A	44.4
Red Bobs	41.4	Red Bobs	3A	41.4
Redman	41.6	Redman	3A	41.6
S615	50.7	S615	3A	48.4
Mean	46.9		Mean	45.7

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	6	28	4.7	1.1
Varieties	4	1,875	468.8	106.5**
Disomics v. Monosomics	1	13	13.0	2.9
Disomics x Monosomics	4	14	3.5	0.8
Error	53	235	4.4	
Total	68	2,165		

L.S.D. at 5% level: 2.1
" " 1% " : 2.7

TABLE XX

THE COMPARISON OF NUMBER OF DAYS TO HEADING OF RECIPROCAL F_1 MONOSOMIC x DISOMIC HYBRIDS INVOLVING CHROMOSOME 3A

Hybrid Combination		Chromosome as Univalent		Mean days to Head	Significance of Difference
Chinese 3A	x Rescue	Rescue	3A	46.7	N.S.
Rescue 3A	x Chinese	Chinese	3A	48.6	
Chinese 3A	x Red Bobs	Red Bobs	3A	42.3	*
Red Bobs 3A	x Chinese	Chinese	3A	45.3	
Chinese 3A	x Redman	Redman	3A	43.7	N.S.
Redman 3A	x Chinese	Chinese	3A	44.3	
Chinese 3A	x S615	S615	3A	51.4	N.S.
S615 3A	x Chinese	Chinese	3A	51.1	
Rescue 3A	x Red Bobs	Red Bobs	3A	41.3	N.S.
Red Bobs 3A	x Rescue	Rescue	3A	40.3	
Rescue 3A	x Redman	Redman	3A	42.4	N.S.
Redman 3A	x Rescue	Rescue	3A	41.6	
Rescue 3A	x S615	S615	3A	50.1	**
S615 3A	x Rescue	Rescue	3A	45.1	
Red Bobs 3A	x Redman	Redman	3A	40.1	N.S.
Redman 3A	x Red Bobs	Red Bobs	3A	41.7	
Red Bobs 3A	x S615	S615	3A	44.9	**
S615 3A	x Red Bobs	Red Bobs	3A	40.4	
Redman 3A	x S615	S615	3A	44.7	N.S.
S615 3A	x Redman	Redman	3A	42.0	

Significant effects at 1% level: S615 > Rescue, Red Bobs

at 5% level: Chinese > Red Bobs

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	6	100	16.7	2.93*
Lines	19	1,698	89.4	15.68**
Error	114	650	5.7	
Total	139	2,448		

L.S.D. on Duncan's Multiple-Range Test at 5% level: 2.5 to 3.1

" 1% " : 3.3 to 4.0

TABLE XXI

THE EFFECT OF THE ABSENCE OF CHROMOSOME 4B ON THE NUMBER OF DAYS TO HEADING OF FOUR WHEAT VARIETIES

Disomic	Mean days to Head	Monosomic		Mean days to Head
Chinese	59.3	Chinese	4B	56.0
Rescue	39.1	Rescue	4B	40.1
Red Bobs	36.3	Red Bobs	4B	35.9
S615	44.1	S615	4B	47.9
Mean	44.7		Mean	45.0

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	6	64	10.7	1.41
Varieties	3	3,768	1,256	165.9**
Disomics v. Monosomics	1	1	1.0	0.13
Disomics x Monosomics	3	89	29.7	39.19**
Error	42	318	7.6	
Total	55	4,240		

L.S.D. at 5% level: 3.2
" " 1% " : 4.1

TABLE XXII

THE COMPARISON OF NUMBER OF DAYS TO HEADING OF RECIPROCAL F_1 MONOSOMIC x DISOMIC HYBRIDS INVOLVING CHROMOSOME 4B

Hybrid Combination		Chromosome as Univalent		Mean days to Head	Significance of Difference
Chinese 4B	x Rescue	Rescue	4B	41.6	*
Rescue 4B	x Chinese	Chinese	4B	45.1	
Chinese 4B	x Red Bobs	Red Bobs	4B	36.7	**
Red Bobs 4B	x Chinese	Chinese	4B	40.6	
Chinese 4B	x S615	S615	4B	50.1	N.S.
S615 4B	x Chinese	Chinese	4B	50.0	
Rescue 4B	x Red Bobs	Red Bobs	4B	36.3	**
Red Bobs 4B	x Rescue	Rescue	4B	40.7	
Rescue 4B	x S615	S615	4B	48.4	*
S615 4B	x Rescue	Rescue	4B	45.4	
Red Bobs 4B	x S615	S615	4B	35.9	**
S615 4B	x Red Bobs	Red Bobs	4B	40.3	

Significant effects at 1% level: Chinese, Rescue Red Bobs

Red Bobs S615

at 5% level: S615 Rescue

Chinese Rescue

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	6	97	16.2	2.51*
Lines	11	2,039	185.4	28.78**
Error	61	393	6.4	
Total	78	2,529		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 2.6 to 3.1
" 1% " : 3.5 to 4.0

ticularly for S615, Rescue and Red Bobs. Chinese 4B seems to induce lateness to head to a greater degree than chromosome 4B of either Rescue or Red Bobs, (Table XXII).

Days to Heading: Chromosome 6B. (Tables XXIII and XXIV) From the monosomic and disomic material, it appears that 6B is not a very important chromosome as far as heading is concerned, (Table XXIII).

In the comparison of the monosomes (Table XXIV) Red Bobs 6B causes significantly later heading than Redman 6B, and Redman 6B causes significantly later heading than S615 6B.

Days to Heading: Chromosome 7D. (Tables XXV and XXVI) The lack of monosomic effect or interaction of the heading date of the varieties tested may indicate that this is not a very important chromosome as far as heading is concerned, (Table XXV).

The significant results in the monosomic comparisons show that Chinese and Redman 7D promote later heading than Rescue 7D, (Table XXVI).

Modifications of the F_1 Method

Nullisomic and disomic crosses. As a result of the late planting date associated with the extremely dry conditions that prevailed during the season, this trial failed to give any useful data for the evaluation of this approach.

Clonal propagation. The trial made up of this material was also planted late and was adversely affected by the drought. The clonal material however did not establish itself well, several of the plants dying and the remainder failing to tiller out, coming rapidly in to head, and being severely attacked by the birds. No results were obtained from this trial.

TABLE XXIII

THE EFFECT OF THE ABSENCE OF CHROMOSOME 6B ON THE NUMBER OF DAYS TO HEADING OF FIVE WHEAT VARIETIES

Disomics	Mean days to Head	Monosomic		Mean days to Head
Chinese	53.8	Chinese	6B	53.7
Rescue	44.0	Rescue	6B	45.1
Red Bobs	40.1	Red Bobs	6B	42.0
Redman	41.1	Redman	6B	42.3
S615	47.8	S615	6B	47.6
Mean	45.4		Mean	46.1

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	11	161	14.6	1.92
Varieties	4	2,592	648.0	85.26**
Disomics v. Monosomics	1	18	18.0	2.37
Disomics x Monosomics	4	19	4.8	0.63
Error	99	752	7.6	
Total	119	3,542		

L.S.D. at 5% level: 6.9
" " 1% " : 9.1

TABLE XXIV

THE COMPARISON OF THE NUMBER OF DAYS TO HEADING OF RECIPROCAL F_1 MONOSOMIC x DISOMIC HYBRIDS INVOLVING CHROMOSOME 6B

Hybrid Combination		Chromosome as Univalent		Mean days to Head	Significance of Difference
Chinese 6B	x Rescue	Rescue	6B	44.8	N.S.
Rescue 6B	x Chinese	Chinese	6B	44.6	
Chinese 6B	x Red Bobs	Red Bobs	6B	42.5	N.S.
Red Bobs 6B	x Chinese	Chinese	6B	41.6	
Chinese 6B	x Redman	Redman	6B	41.8	N.S.
Redman 6B	x Chinese	Chinese	6B	42.3	
Chinese 6B	x S615	S615	6B	47.6	N.S.
S615 6B	x Chinese	Chinese	6B	48.0	
Rescue 6B	x Red Bobs	Red Bobs	6B	40.6	N.S.
Red Bobs 6B	x Rescue	Rescue	6B	40.8	
Rescue 6B	x Redman	Redman	6B	41.6	N.S.
Redman 6B	x Rescue	Rescue	6B	41.3	
Rescue 6B	x S615	S615	6B	45.2	N.S.
S615 6B	x Rescue	Rescue	6B	45.7	
Red Bobs 6B	x Redman	Redman	6B	41.1	**
Redman 6B	x Red Bobs	Red Bobs	6B	44.3	
Red Bobs 6B	x S615	S615	6B	41.3	N.S.
S615 6B	x Red Bobs	Red Bobs	6B	42.4	
Redman 6B	x S615	S615	6B	42.3	**
S615 6B	x Redman	Redman	6B	44.9	

Significant effects at 1% level: Red Bobs Redman

Redman S615

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	11	459	41.7	21.38**
Lines	19	1,155	60.8	31.17**
Error	205	399	1.95	
Total	235	2,013		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 1.1 to 1.4
" 1% " : 1.5 to 1.8

TABLE XXV

THE EFFECT OF THE ABSENCE OF CHROMOSOME 7D ON THE NUMBER OF DAYS TO HEADING OF FOUR WHEAT VARIETIES

Disomic	Mean days to Head	Monosomic		Mean days to Head
Chinese	55.5	Chinese	7D	47.9
Rescue	42.7	Rescue	7D	43.0
Red Bobs	38.3	Red Bobs	7D	39.7
Redman	38.3	Redman	7D	38.7
Mean	43.7		Mean	42.3

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	106	21.2	3.46*
Varieties	3	2,280	760.0	126.67**
Disomics v. Monosomics	1	3	3.0	0.49
Disomics x Monosomics	3	3	1.0	0.16
Error	34	207	6.1	
Total	46	2,599		

L.S.D. at 5% level: 2.8
" " 1% " : 3.6

TABLE XXVI

THE COMPARISON OF THE NUMBER OF DAYS TO HEADING OF RECIPROCAL F_1 MONOSOMIC x DISOMIC HYBRIDS INVOLVING CHROMOSOME 7D

Hybrid Combination		Chromosome as Univalent		Mean days to Head	Significance of Difference
Chinese 7D	x Rescue	Rescue	7D	41.8	**
Rescue 7D	x Chinese	Chinese	7D	44.7	
Chinese 7D	x Red Bobs	Red Bobs	7D	39.2	N.S.
Red Bobs 7D	x Chinese	Chinese	7D	40.7	
Chinese 7D	x Redman	Redman	7D	40.0	N.S.
Redman 7D	x Chinese	Chinese	7D	41.2	
Rescue 7D	x Red Bobs	Red Bobs	7D	38.7	N.S.
Red Bobs 7D	x Rescue	Rescue	7D	40.8	
Rescue 7D	x Redman	Redman	7D	42.5	**
Redman 7D	x Rescue	Rescue	7D	39.5	
Red Bobs 7D	x Redman	Redman	7D	38.2	N.S.
Redman 7D	x Red Bobs	Red Bobs	7D	38.8	

Significant effects at 1% level: Redman, Chinese > Rescue

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	146	19.2	6.00**
Lines	11	230	20.9	6.53**
Error	53	172	3.2	
Total	69	548		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 2.1 to 2.5
" 1% " : 2.8 to 3.2

F_3 Bulk Method

Grain yield. For reasons previously discussed, yield determinations were only available for two of the trials that were sown to test this method. These were the F_3 bulk field trial sown in the spring of 1960, and the greenhouse F_3 bulk trial. The analysed results of these trials are presented in Tables XXVII and XXVIII. There appears to be some difference in response of the lines tested to the markedly contrasting growing conditions to which the two trials were exposed. In the greenhouse trial, the earlier maturing lines, most noticeably the variety Thatcher, were induced by the high temperatures experienced during the early growing period to head out rapidly, apparently at the expense of tillering. The yield of these early lines was reduced as a consequence. The performance of the substitution lines and parental varieties in the field sown trial is in general agreement with the published results (22) for this material.

A comparison of the yield of the substitution lines with the variety Chinese indicates that some of the substituted Thatcher chromosomes are an important influence in the improvement of yield, chromosome 1B being the most significant and consistent in this respect. The yielding ability of the substituted bulks however is in no case significantly superior to the parental F_3 bulk, but in some cases is markedly inferior. There is no relationship between the influence of the Thatcher substituted chromosomes on the yielding ability of Chinese on the one hand and the changes in the F_3 bulk population due to the establishment of a pair of Thatcher chromosomes in the pure state, on the other.

TABLE XXVII

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON GRAIN YIELD OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS, AS TESTED IN A REPLICATED FIELD TRIAL

Variety or Substitution	Mean yield in gm.	Difference from Chinese	F_3 Hybrid Bulk	Mean yield in gm.	Difference from variety bulk mean
Chinese	287.3		Chinese x Thatcher A	458.2	
Thatcher	484.0		" x " B	427.0	
Substitution 1B	420.7	+133.4**			
" 3A	326.0	+ 38.7	Substituted Bulk 3A	451.7	+ 9.1
" 4B	374.7	+ 87.4*			
" 5A	366.0	+ 78.7*	" " 5A(A)	508.3	+65.7
			" " 5A(B)	494.8	+52.2
" 6B	305.2	+ 17.9	" " 6B	445.7	+ 3.1
" 7D	404.3	+117.0**			

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	63,732	12,746	3.41**
Lines	13	386,215	29,708	7.95**
Error	65	242,966	3,738	
Total	83	692,913		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 67.9 to 84.8
" 1% " : 93.6 to 110.5

TABLE XVIII

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON GRAIN YIELD OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS AS TESTED IN A REPLICATED GREENHOUSE TRIAL

Variety or Substitution	Mean yield in gm.	Difference from Chinese	F_3 Hybrid Bulk	Mean yield in gm.	Difference from variety bulk
Chinese	21.7		Chinese x Thatcher A	34.4	
Thatcher	26.4				
Substitution 1B	42.0	+20.3**	Substituted Bulk 1B	22.7	-11.7**
" 3A	40.8	+19.1**	" " 3A	29.9	- 4.5
" 4B	26.7	+ 5.0	" " 4B	24.7	- 9.7**
" 5A	26.1	+ 4.4	" " 5A(A)	36.8	+ 2.4
" 6B	27.1	+ 5.4*	" " 6B	36.0	+ 1.6
" 7D	21.2	- 0.5	" " 7D	22.9	-11.5**

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	107.0	21.41	1.00
Lines	14	4,081.9	291.56	13.61**
Error	70	1,499.4	21.42	
Total	89	5,688.3		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 5.3 to 6.4
" 1% " : 7.1 to 8.4

Kernel weight. As was the case with grain yield, material for the estimation of kernel weight was available from only two of the trials sown. The analysis of these data (Tables XXIX and XXX), indicates rather substantial differences between the lines under test. The incorporation of Thatcher chromosomes into both the Chinese background and also into the segregating genetic background of the F_3 bulks had in most cases the effect of producing heavier grain. The magnitude of the increase was generally greater in the substitution lines.

From the study of kernel weight there seems to be some slight evidence of similarity of action of the chromosomes in the two diverse backgrounds of the variety Chinese and the segregating F_3 bulk. The correspondence is by no means exact, however, and in some cases contradictory results are obtained.

Days to Heading. Information on this character was obtained from all the trials and observation plots planted for the purposes of the evaluation of the F_3 bulk method. There was a practical difficulty involved in estimating this character, as in the plots of segregating material there was often considerable variation amongst the plants of a single plot. The results are presented in Tables XXXI to XXXV.

Consistency of heading for the parental varieties and the substitution lines was observed in the trials involving the Chinese and Thatcher combinations, chromosomes 1B, 3A and 4B of Thatcher each inducing significantly earlier heading of the substitution lines in each trial carried out. However, the bulks containing the substituted chromosomes in the pure state closely resembled the variety F_3 bulk as

TABLE XXIX

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON THE KERNEL WEIGHT OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS AS TESTED IN A REPLICATED FIELD TRIAL

Variety or Substitution	Mean weight of 200 kernels in gm.	Difference from Chinese	F_3 Hybrid Bulk	Mean weight of 200 kernels in gm.	Difference from variety bulk mean
Chinese	3.27		Chinese x Thatcher Bulk A	5.15	
Thatcher	5.73		" x " Bulk B	5.15	
Substitution 1B	5.32	+2.05**			
" 3A	4.01	+0.74**	Substituted Bulk 3A	5.27	+0.12
" 4B	4.31	+1.04**			
" 5A	3.91	+0.64**	" " 5A(A)	5.33	+0.18*
			" " 5A(B)	5.59	+0.44**
" 6B	3.51	+0.24**	" " 6B	5.22	+0.07
" 7D	4.22	+0.95**			

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	2.42	0.48	3.00*
Varieties	13	48.80	3.75	23.44**
Error	65	10.34	0.16	
Total	83	61.66		

L.S.D. on Duncan's Multiple-Range Test
at 5% levels .14 to .17
" 1% " : .19 to .22

TABLE XXX

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON THE KERNEL WEIGHT OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS AS TESTED IN A REPLICATED GREENHOUSE TRIAL

Variety or Substitution	Mean weight of 200 kernels in gm.	Difference from Chinese	F_3 Hybrid Bulk	Mean weight of 200 kernels in gm.	Difference from variety bulk
Chinese	3.58		Chinese x Thatcher Bulk A	4.62	
Thatcher	4.94				
Substitution 1B	4.69	+1.11**	Substituted Bulk 1B	4.46	-0.16**
" 3A	4.88	+1.30**	" " 3A	4.83	+0.21**
" 4B	4.49	+0.91**	" " 4B	5.13	+0.51**
" 5A	3.66	+0.08**	" " 5A(A)	4.83	+0.21**
" 6B	3.63	+0.05**	" " 6B	4.90	+0.28**
" 7D	3.56	-0.02	" " 7D	4.64	+0.02

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	0.21	0.04	1.33
Varieties	14	25.86	1.85	61.67**
Error	70	1.78	0.03	
Total	89	27.85		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: .02
" 1% " : .03

TABLE XXXI

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON THE HEADING DATE OF SUBSTITUTION LINES AND SUBSTITUTED F_3 BULKS AS TESTED IN A REPLICATED TRIAL

Variety or Substitution	Mean days to head	Difference from Chinese	F_3 Hybrid Bulk	Mean days to head	Difference from variety bulk mean
Chinese	63.5		Chinese x Thatcher A	51.7	
Thatcher	49.0		" x " B	51.7	
Substitution 1B	49.7	-13.8**			
" 3A	60.8	- 2.7*	Substituted Bulk 3A	52.7	+1.0
" 4B	59.8	- 3.7**			
" 5A	61.5	- 2.0	" " 5A(A)	51.2	-0.5
			" " 5A(B)	51.2	-0.5
" 6B	62.8	- 0.7	" " 6B	52.0	+0.3
" 7D	62.3	- 1.2			

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	106	21.2	6.24**
Varieties	13	2,464	189.5	55.74**
Error	65	218	3.4	
Total	83	2,788		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 2.1 to 2.6
" 1% " : 2.8 to 3.3

TABLE XXXII

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON DAYS TO HEAD OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS AS TESTED IN A REPLICATED GREENHOUSE TRIAL

Variety or Substitution	Mean days to head	Difference from Chinese	F_3 Hybrid Bulk	Mean days to head	Difference from variety bulk
Chinese	60.5		Chinese x Thatcher Bulk A	43.7	
Thatcher	40.0				
Substitution 1B	43.7	-16.8**	Substituted Bulk 1B	46.7	+3.0*
" 3A	53.9	- 6.6**	" " 3A	42.7	-1.0
" 4B	51.9	- 8.6**	" " 4B	46.2	+2.5*
" 5A	59.5	- 1.0	" " 5A(A)	41.2	-2.5*
" 6B	57.9	- 2.6*	" " 6B	42.0	-1.7
" 7D	59.3	- 1.2	" " 7D	46.3	+2.6

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	5	130	26.0	6.52**
Varieties	14	4,606	329.0	82.46**
Error	70	279	4.0	
Total	89	5,015		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 2.3 to 2.8
" 1% " : 3.1 to 3.7

TABLE XXXIII

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON DAYS TO HEAD OF SUBSTITUTION LINES AND F_4 SUBSTITUTED BULKS AS TESTED IN A FIELD TRIAL

Variety or Substitution	Mean days to head	Difference from Chinese	F_4 Hybrid Bulk	Mean days to head	Difference from variety bulk mean
Chinese	65.0		Chinese x Thatcher A	52.2	
Thatcher	47.4		" x " B	51.2	
Substitution 1B	50.0	-15.0**			
" 3A	58.4	- 6.6**	Substituted Bulk 3A	50.0	-1.7
" 4B	57.6	- 7.4**			
" 5A	62.0	- 3.0**	" " 5A(A)	51.4	-0.3
			" " 5A(B)	48.8	-2.9 *
" 6B	60.2	- 4.8**	" " 6B	50.8	-0.9
" 7D	59.2	- 5.8**			

Source of variation	d.f.	Sum of Squares	Mean Square	F
Replications	4	16	4.0	1.43
Varieties	13	2,043	157.0	56.07**
Error	52	148	2.8	
Total	69	2,207		

L.S.D. on Duncan's Multiple-Range Test
at 5% level: 2.1 to 2.6
" 1% " : 2.8 to 3.4

TABLE XXXIV

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON DAYS TO HEAD OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS AS TESTED IN FIELD OBSERVATION PLOTS

Variety or Substitution	Days to head	Difference from Chinese	F_3 Hybrid Bulk	Days to head	Difference from variety bulk
Chinese	59		Chinese x Thatcher	45	
Thatcher	42				
Substitution 1B	47	-12	Substituted Bulk 1B	45	0
" 4B	56	- 3	" " 4B	46	+1
" 7D	59	0	" " 7D	44	-1

far as heading date was concerned in the two field trials. There was little or no correspondence between the influence of the Thatcher chromosomes in the substitution lines and the same chromosomes in the bulk populations.

The information obtained from the observation plots of the Rescue 5A hybrid bulks differed rather in nature from that of the foregoing trials, in that the appropriate substitution lines were not available. Thus this test is more an evaluation of the influence of chromosome 5A obtained from different sources on the time of heading. As two observation plots of each line were sown, the results listed in Table XXXV are the mean of the two plots. The impression gathered from this test is that the presence of chromosome 5A donated by one of the varieties in the paired state does not exert a very strong influence on time to

TABLE XXXV

THE INFLUENCE OF CHROMOSOME 5A FROM DIFFERENT VARIETIES ON DAYS TO HEAD OF F_3 SUBSTITUTED BULKS AS TESTED IN FIELD OBSERVATION PLOTS

Variety or F_3 Variety Bulk	Mean days to head	F_3 Substituted Bulk	Mean days to head	Difference
Rescue	49.5			
Rescue x Redman	46.0	Rescue 5A x Redman	45.0	-1.0
" x Red Bobs	42.5	" 5A x Red Bobs	42.5	0
" x S615	49.5	" 5A x S615	52.0	+2.5
" x Pembina	44.0	" 5A x Pembina	42.5	-1.5
" x Thatcher	44.0	" 5A x Thatcher	43.0	-1.0
" x Chinese	49.5	" 5A x Chinese	50.5	+1.0
" x Aotea	56.5	" 5A x Aotea	59.0	+2.5

heading in the substituted bulk. This may be because chromosome 5A of the lines tested does not have a very important effect on heading date, though Kuspira and Unrau (22) found that this chromosome was effective in inducing earlier maturity in three substitution lines they studied, or alternatively that the F_3 bulk method does not reveal these diffefences.

Plant Height. As was the case with the measurement of heading date, the determination of plant height was made difficult by within plot variation of the bulk lines. For reasons of this variation the plots were placed in 3 inch height categories with respect to this character. Results were obtained from three trials and two sets of observation plots, and these are presented in Tables XXXVI to XL. Owing to the crude

nature of the determinations, the results were not analysed, the mean class value being chosen as the representative value of the line concerned. By the very nature of the method of measurement, only gross differences in height were revealed. Of the substitution lines only chromosome 4B seemed to be consistently shorter, and in the bulk populations, few plots differed from the values determined for the variety hybrid bulk. There seemed to be no tendency, as far as could be established, for the results of the substituted bulks to agree with those obtained by the comparison of the substitution line and the variety Chinese. Similarly in the observation plots of Rescue hybrids, only minor height differences were observed.

TABLE XXXVI

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON PLANT HEIGHT OF SUBSTITUTED LINES AND F_3 SUBSTITUTED BULKS AS TESTED IN A REPLICATED FIELD TRIAL

Variety or Substitution	Mean plant height group	Difference from Chinese	F_3 Hybrid Bulk	Mean plant height group	Difference from variety bulk mean
Chinese	3'0" to 3'3"		Chinese x Thatcher Bulk A	3'0"	
Thatcher	3-0		" x " " B	3-0 to 3-3	
Substitution 1B	3-0	=			
" 3A	3-0	=	Substituted Bulk 3A	3-0	=
" 4B	2-9	- 3"			
" 5A	3-0	=	" " 5A(A)	2-9 to 3-0	=
			" " 5A(B)	3-0 to 3-3	=
" 6B	3-0 to 3-3	=	" " 6B	3-3	=
" 7D	3-0	=			

TABLE XXXVII

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON PLANT HEIGHT OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS, AS TESTED IN A REPLICATED GREENHOUSE TRIAL

Variety or Substitution	Mean plant height group	Difference from Chinese	F_3 Hybrid Bulk	Mean plant height group	Difference from variety bulk
Chinese	3'-3"		Chinese x Thatcher Bulk A	3'-0" to 3'-3"	
Thatcher	2-9				
Substitution 1B	3-0 to 3-3	=	Substituted Bulk 1B	3-0	=
" 3A	3-3 to 3-6	=	" " 3A	3-0	=
" 4B	3-0	-3"	" " 4B	3-0	=
" 5A	3-0	-3"	" " 5A(A)	3-0	=
" 6B	3-3	=	" " 6B	3-0	=
" 7D	3-0	-3"	" " 7D	3-0	=

TABLE XXXVIII

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON PLANT HEIGHT OF SUBSTITUTION LINES AND F_4 SUBSTITUTED BULKS AS TESTED IN A REPLICATED FIELD TRIAL

Variety or Substitution	Plant height group	Difference from Chinese	F_4 Hybrid Bulk	Plant height group	Difference from variety bulk mean
Chinese	3'-0"		Chinese x Thatcher Bulk A	2'-9"	
Thatcher	2-3		" x " " B	3-0	
Substitution 1B	2-6	-6"			
" 3A	3-0	=	Substituted Bulk 3A	2-9	=
" 4B	2-9	-3"			
" 5A	3-0	=	" " 5A(A)	2-6	-3"
			" " 5A(B)	2-6	-3"
" 6B	2-9	-3"	" " 6B	2-9	=
" 7D	3-0	=			

TABLE XXXIX

THE INFLUENCE OF CERTAIN THATCHER CHROMOSOMES ON PLANT HEIGHT OF SUBSTITUTION LINES AND F_3 SUBSTITUTED BULKS AS TESTED IN FIELD OBSERVATION PLOTS

Variety or Substitution	Plant height group	Difference from Chinese	F_3 Hybrid Bulk	Plant height group	Difference from variety bulk
Chinese	3'-0"		Chinese x Thatcher Bulk	3'-9"	
Thatcher	3-0				
Substitution 1B	3-6	+6"	Substituted Bulk 1B	3-6	-3"
" 4B	3-3	+3"	" " 4B	3-6	-3"
" 7D	3-6	+6"	" " 7D	3-6	-3"

TABLE XL

THE INFLUENCE OF CHROMOSOME 5A FROM DIFFERENT VARIETIES ON PLANT HEIGHT OF F_3 SUBSTITUTED BULKS AS TESTED IN FIELD OBSERVATION PLOTS

Variety or F_3 Variety Bulk	Mean plant height group	F_3 Substituted Bulk	Mean plant height group	Difference between variety and substituted bulks
Rescue	3'-6"			
Rescue x Redman	3-3	Rescue 5A x Redman	3'-3" to 3'-6"	=
" x Red Bobs	3-6 to 3-9	" 5A x Red Bobs	3-6 to 3-9	=
" x S615	3-6 to 3-9	" 5A x S615	3-3 to 3-6	=3"
" x Pembina	3-3	" 5A x Pembina	3-0	-3"
" x Thatcher	3-3 to 3-6	" 5A x Thatcher	3-3	=
" x Chinese	3-3 to 3-6	" 5A x Chinese	3-3	=
" x Aotea	3-0 to 3-3	" 5A x Aotea	3-0	=

DISCUSSION

The advantages of a reliable method of early generation testing as a means of prompt elimination from a breeding programme of such materials that will not provide the plant breeder with the required combinations of characteristics, is obvious. It enables greater concentration of effort to be directed to the lines that are likely to yield the desired types, as well as being valuable from the viewpoint of economy of time and labour. Consequently a number of attempts to find a method have been made, particularly on such economically important crops as the cereal grains, soybeans and corn. Attempts of this nature directed towards the self-fertilizing crops have led to the opinion, if one may generalize from such a number of divergent opinions, that although early generation testing is of some predictive value for simply inherited characters, it has little chance of success for characters of such complex inheritance and low heritability as grain yield. These methods, using the mean performance of early segregating generations as a basis for selection, do not take into account the importance of a large range of genetic diversity in the character under investigation. Instead, a line of high mean performance is selected, although the range of variation in this line may well be very limited.

In the application of early generation testing to corn breeding, an improvement of the method was possible in that individuals were selected from the population on the basis of a performance test. Thus the change was made from discrimination between populations to sampling within a diverse population by means of a test cross, with the segre-

gation of only the individuals selected to be considered.

This project extends the scope of early testing into the field of chromosome substitution in wheat, and though the experimental material for this study is self-pollinating, the tests involved are more akin to those applied to corn than those applied to the small grains.

There has been a recent tendency to apply such corn-breeding terms as combining ability and heterosis to investigations in the self-pollinated crops (24). If we apply these concepts to the methods studied in this project, the F_1 method may be thought to be a test of specific combining ability of single chromosomes against a standard genetical background. If a chromosome of one variety shows to advantage in these tests, we may look upon it as carrying a favourable gene complex and being a good combiner.

In contrast to the F_1 method, the F_3 bulk method of chromosome evaluation may be thought to be a test of general combining ability, in which the donated chromosome is tested against the multiplicity of genotypic backgrounds present in a segregating population. The chromosome is not being tested against the genetic background with which it will be combined in the substitution line, although the components of this background are present in the segregating bulk population. If the favourable action of the chromosome in the substitution line is the result of a genetic interaction between it and the genetic background, this may be a disadvantage.

In the trials that were studied to test the F_1 method for the prediction of grain yield potential, the absence of chromosomes 1B and 3A from the varieties used, as tested in the comparison of the varieties

in the monosomic and disomic condition, was accompanied by a reduction of yield, and all varieties reacted in a similar manner to the deficiency. In the comparison of the reciprocal monosomic x disomic hybrid lines, some very marked differences between homologous chromosomes of different varieties were found for this character. In the trial involving chromosome 1B for example, clear superiority of Redman chromosome 1B over its homologues in the other three varieties tested is demonstrated, while for chromosome 3A it seems that S615 is distinctly inferior to most of the other 3A chromosomes.

If the varieties used in the trial of chromosome 1B are ranked with respect to the performance of this chromosome, without reference to statistical significance of the differences (although all the differences at least approach significance), the varieties can be listed in a linear order of performance as follows.

Chromosome 1B: Redman > Rescue > Chinese > Red Bobs

A similar linear ranking in performance is also evident in the trial involving chromosome 3A in which five varieties are involved, and though again the results show no exceptions, in some cases the differences are small.

Chromosome 3A: Red Bobs > Rescue > Chinese > Redman > S615

All the results obtained are consistent with this sequence. If the number of genes influencing yield is large, as seems likely, the above would not represent an unexpected result, and would provide precisely the type of information that the method was designed to reveal. The es-

tablishment of this result at a statistically significant level may only require refinement of the field techniques used, or the processing of more material.

That the yield differences found between the reciprocal pairs of the monosomic x disomic pairs is due to the chromosome in the monosomic condition is attested to by the fact that the analysis of yield of the disomic hybrids failed to reveal any differences between the reciprocals. This would indicate that the genetical backgrounds of the monosomic x disomic hybrid reciprocal pairs did not make any differential contribution to yield.

In the use of the characteristic of heading date to evaluate the F_1 method, results from trials of five different chromosome lines were available. In the testing of the varieties in the disomic versus the monosomic condition, only one chromosome, 1B showed a significant effect, the monosomics as a group being later to head. The analysis of the monosomic x disomic hybrids however, reveals some differences, chromosome 4B being the most active in this respect. There is again a tendency for the varieties to array themselves in the manner already discussed for the chromosome being investigated, though it is less marked than in the results for yield and some contradictory results occur. The absence of reciprocal differences between the disomic hybrids makes it seem likely that the differences between the monosomic x disomic reciprocals are due to the monosomes involved.

To summarize it appears that this method warrants further investigation, though a final assessment of its value will not be able to be made until the appropriate substitutions are made and their performance

compared with the predicted results.

A number of other aspects of the method must also be considered, whether testing chromosomes in the monosomic condition or against a hybrid genetical background has particular influence on the results, and also the relationship must be established for yielding values of plants under conditions of the wide spacing used in the trials with the close competition under which the substitution lines are tested.

A further extension of the work would be towards the establishment of a series of testers with which varieties could be combined to establish their potential as sources of chromosomes for substitution, thus reducing the work involved in the setting up of a complete trial.

Unfortunately the two modifications of the F_1 method tested failed to yield results but under different conditions these approaches may have yielded useful information.

Before an evaluation of the F_3 bulk test is made, it must be decided to what extent the comparisons of substitution and variety with substituted and variety bulks must be in accord before validity for the method can be claimed. If it is to be a useful plant breeding tool, the method would have to react consistently for all varieties and all chromosomes tested with respect of direction of the change in the character (whether it was increased or decreased), as well as giving some indication of the magnitude of the change. Against these rather stringent requirements, the method has not measured up well for the varieties, chromosomes and characters studied. The necessary correspondence between the lines tested has not been observed, the substituted bulks in general resembling too precisely the variety bulks for the characters tested.

This may well be due to a fundamental difference in the lines upon which the tests were made. In the case of the substitution line being compared with the parental variety, the comparison is in essence an evaluation of a pair of Thatcher chromosomes against the homologous pair from Chinese. In the assessment of the performance of the substituted bulk against the varietal bulk, however, the comparison is between a pair of Thatcher chromosomes and a pair of homologous chromosomes contributed to both by Thatcher and Chinese.

Although due to crossing over the contribution of the individual varieties to the hybrid chromosome pair probably would vary within wide limits, the average contribution over the whole population should be equal by each parent. Thus a pair of Thatcher chromosomes are being assessed against a chromosome pair, half of which is also from Thatcher, and the deviations of the characters studied are likely to be less in the bulks than in the case of the substitution line with the recurrent variety. In addition, if the genes governing the character studied are completely dominant, and carried on the Thatcher chromosome, then the single dose of the Thatcher chromosome in the hybrid pair would be sufficient for full expression of the character in the varietal bulk, and no difference between the two bulks would be observed.

In the F_3 trials in which duplicate variety bulks and bulks for chromosome 5A were included (Tables XXVII and XXXI), the absence of significant differences between the pairs of bulks would seem to indicate that the sample of fifty F_2 plants per bulk was sufficient to give an adequate sampling of the variation of the F_2 population.

The progeny of the F_3 bulks used in the trials can be used in

following generations to further test the method, as in the substituted bulks the Thatcher chromosome pair maintain their identity. The selective influence of the environment, or other factors may change the composition and performance of the rest of the genotype however.

Continued growing of these substituted bulks through a number of generations would finally lead to populations of homozygous lines, each line carrying the same pair of Thatcher chromosomes. This process could be adapted to plant breeding purposes if it was thought expedient to retain a chromosome of a particular variety in a pure state, perhaps for reason of genes for disease resistance, in every member of a heterogeneous population such as is used in the hybrid bulk breeding method.

CONCLUSIONS

1. The F_1 method of testing whole chromosomes demonstrated differences between homologous chromosomes of the varieties tested, in their contribution to the plant characters studied.

2. This method warrants further investigation as a means of selecting chromosomes for whole chromosome substitution.

3. The F_3 bulk method did not reveal the influence substituted chromosomes in bulk populations as demonstrated by the performance of the appropriate substitution lines.

4. The F_3 bulk method does not seem to have any application as a means of selecting chromosomes for substitution.

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