group. This ability accounts for the occurrence of specific trisomics among the self progeny of a particular nullisomic that sets seed, exclusive of nullisomic 3B (3) which has a high frequency of asynapsis. Also in a nullisomic plant, microspores with an extra chromosome are favored when that chromosome compensates at least in part for the missing one.

The pairs with satellites and secondary constrictions were identified as chromosomes 1 and 10 (Morrison 1953). Chromosome 1 is the longer of the two, is the more heterobrachial, and has the smaller satellite. Reference to the above list shows they belong to the B genome. Since T. monococcum with the A genome has two pairs with satellites (Burnham, unpublished), the satellites must be suppressed in hexaploid wheat or they have been lost.

Certain varieties of T. vulgare wheat differ from the Chinese variety by one or more interchanges. The Thatcher variety has an interchange between chromosomes 4 and 10. New interchanges have appeared also in the 2n progeny from haploid Triticum vulgare (Sears and Okamoto 1958). These would be expected if exchange occurs between the chromosomes that occasionally pair in the haploid. The chromosomes of 13 of those interchanges have been identified. Nine of them were between homoeologs, four were not. These results indicate that association and exchange are not at random, but are more likely to involve homoeologs, although not exclusively so.

Special methods of locating genes

The number of useful qualitative genetic characters in wheat is limited. There is only one chlorophyll mutant (Neatby's virescent), no good endosperm characters, probably three factors for seed color; several head characters including hooded, awnless, dense (compactoid), glume shape (speltoid); and several plant characters, coleoptile and stem color, pubescent node, glossy sheath, and liguleless. In addition there are the factors for disease resistance, e.g. for stem and leaf rust, mildew, and bunt. The F_2 ratios for certain of these characters in normal hexaploid wheat are 3:1; for others, including many of the leaf and stem rust reactions to individual races, there are also other types of interactions of two factor pairs resulting in 9:7, 15:1 or 13:3 ratios with resistance dominant in certain cases, recessive in others (Hayes et al.). Resistance to the large number of races of rust may be governed by many genes. For example, in a study of leaf rust resistance, not using monosomics, Martinez et al. (1953) found evidence of six different genes, each segregating 3:1 for reaction to a particular race, but closely linked, the total distance being about six units. The reaction to other races in this same study appeared to be governed by two or more factors. In certain varieties the reaction to a single race of stem rust may be governed by several factors (Plessers 1954, Pi 1961).

With such a limited number of genetic markers, practically no progress had been made in establishing linkage groups. The monosomics have made it possible to accomplish this in wheat.

A list of the characters and the chromosomes on which major genes are located is in Table 115.

Factors have been located in 20 of the 21 chromosomes. Factors for stem rust resistance effective from the seedling stage on to later stages have been found in 11 chromosomes. In general, the methods used in locating these factors and the expected ratios are similar to those described for Nicotiana tabacum (page 228). In wheat there seems to be a more uniform rate of transmission; also nullisomic offspring are usually obtained in the self progeny of a monosomic.

Table 115. List of major genes for wheat characters located mainly by the use of nullisomics, monosomics and substitution lines. A, B, D refer to the genomes. (Selected from lists of Morris, 1959, 1960, 1961; Sears, Personal Comm.)

Variety Source		Character	Location	Method	Authority
Indian, Sonora	Pg	pubescent glumes	1A	nulli.	Sears 1953; Kuspira and Unrau 1960
Indian		black glumes	1A	linkage	Sears (unpub.)
NP 790		stem-rust resistance	1A	mono.	Singh and Swaminathan 1960
Indian		mildew resistance	1A	subst.	Sears and Briggle (unpub.)
Federation 41		brown glume color	1B	mono.	Unrau 1950
T. spelta	Pt	procumbent stem	1D	nulli.	Yamashita 1947, Matsumura 1947
Hope		stem-rust resistance	1D*	subst.	Sears et al. 1957
Kharkov, Jones Fife	Ne_2	Complem. semi-lethal (necrosis)	2A	mono.	Tsunewaki 1960
Redman		complem. dwarf (4B)**	2A	mono.	Hurd and McGinnis 1958
		waxy leaf bloom	2A	mono.	Allan 1959
Red Egyptian, K. Farmer	Sr9	stem-rust resistance	2A	subst.	Sears et al. 1957, Sheen 1962
Redman		stem-rust resistance	2A	mono.	Campbell and McGinnis 1958
Thatcher		stem-rust resistance	2A	subst.	Sears et al. 1957
CI 12633		stem-rust resistance	2A	mono.	Nyquist 1957
Martin		bunt resistance	2A	subst.	Sears et al. 1960
CI 12633		mildew resistance	2A	linkage	Nyquist 1957
Chinese Spring		hollow stem	2A	mono.	Larson 1959
NP 790		stem-rust resistance	2A	mono.	Singh and Swaminathan 1960
Hymar, Little Club	C	compactum (club) head type	2D	mono.	Unrau 1950
Red Egyptian, K. Farmer	Sr_6	stem-rust resistance	2D	subst.	Sears et al. 1957, Sheen 1962
S-615		hollow stem (inhibitor of pith)	2D	mono.	Larson and MacDonald 1959
	v	Neatby's virescent	3B*	mono.	Sears 1953, 1954
Hope		brown necrosis (pseudo black-chaff)	3B	subst.	Kuspira and Unrau 1958
Thatcher, Redman		stem-rust resistance	3B	subst.	Sears et al. 1957, Campbell and McGinnis 1958
Hope		adult-plant stem-rust resistance	3B	subst.	Kuspira and Unrau 1958
S-615		solid stem, top internode	3B	mono.	Larson and MacDonald 1959
Chinese		red seed	3D	nulli.	Sears 1944
T. sphaerococcum	sp	sphaerococcum	3D*	mono.	Sears 1947
Chinese	Ne_3	complem. semi-lethal (necrosis)	3D	mono.	Tseunewaki and Kihara 1961
NP 790		stem-rust resistance	3D	mono.	Singh and Swaminathan 1960
S-615		solid stem, top internode	3D	mono.	Larson and MacDonald 1959
Rye	Hp_1	hairy peduncle	4A*	mono.	Sears (unpub.).
Klein Cometa		stripe-rust resistance	4A	mono.	Singh and Swaminathan 1959
Chinese	Hd	hooded	4B*	nulli.	Sears 1944
Redman		dwarf (complem. gene 2A)**	4B	mono.	Hurd and McGinnis 1958
K. Farmer	Sr_7	stem-rust resistance	4B	mono.	Loegering and Sears (unpub.) Sheen 1962
Redman		stem-rust resistance	4B	mono.	Campbell and McGinnis 1958
Hope		stem-rust resistance	4B	subst.	Sears et al. 1957

Chinese	Q	speltoid suppression, squarehead	5A*	mono.	Sears 1944
Chinese		pubescent nodes (dom.)	5A*	nulli.	Sears 1944
Hymar	sg_2	winter habit	5A*	mono.	Unrau
Marquis, etc.	B_1	awn inhibitor	5A*	linkage	Sears 1944
Klein Cometa		stripe-rust resistance	5A	mono.	Singh and Swaminathan 1959
S-615, Rescue		solid culm, lower internodes	5A	mono.	Larson and MacDonald 1959, 1962
Prelude, T. macha	Ne_1	complem. semi-lethal (necrosis)	5B	mono.	Tsunewaki 1960
Rye	Hp_2	hairy peduncle	5B*	cytol.	Sears (unpub.)
Chinese, Holdfast		reduction in homoeologous pairing	5B*	def.hybr.	Okamoto 1957
				def.hapl.	Riley 1958, Riley *et al*. 1960
S-615		solid culm, lower internodes	5B	mono.	Larson and MacDonald 1959
Kharkov	sg_1	winter growth habit	5D	subst.	Kuspira and Unrau 1957
S-615		solid culm, lower internodes	5D	mono.	Larson and MacDonald 1959
Red Egyptian	Sr_8	stem-rust resistance	6A	subst.	Sears *et al*. 1957
Frontana		stem-rust resistance	6A	mono.	Burnham *et al*. 1953
Klein Cometa		stripe-rust resistance	6A	mono.	Singh and Swaminathan 1959
S615, Rescue		hollow stem (inhibitor of pith)	6A	mono.	Larson and MacDonald 1959, 1962
Chinese	Ki	killer, lethal to ki microspores	6B*	linkage	Sears and Loegering 1961
Chinese	B_2	awn inhibitor	6B*	nulli.	Sears 1944
Chinese	co	corroded (irreg. leaf necrosis)	6B*	mono.	Sears (unpub.)
Timstein	Sr_{11}	stem-rust resistance	6B*	mono.	Sears and Rodenhiser 1948
Transfer (Chin.T47)		leaf-rust resistance (Ae.umbellulata)	6B*	cytol.	Sears 1961
Pawnee		leaf-rust resistance	6B*	mono.	Livers 1949
Chinese		adult-plant leaf-rust resistance	6B	subst.	Unrau (unpub.)
Thatcher	Sr_5	stem-rust resistance (Kanred gene)	6D	subst.	Sears *et al*. 1957
S-615		hollow stem	6D	mono.	Larson and MacDonald 1959
Hope	Re_1	red coleoptile	7A	mono.	Sears 1954
Axminster		mildew resistance	7A	mono.	S. and Rodenhiser, in Sears 1954
S-615		hollow stem (inhibitor of pith)	7A	mono.	Larson and MacDonald 1959
Hope	Pc	purple culm	7B	subst.	Kuspira and Unrau 1960
Hope		earliness	7B	subst.	Kuspira and Unrau 1958
S-615		hollow stem	7D	mono.	Larson and MacDonald 1959

* located to arm by use of telocentric or isochromosome.

** Kenya Farmer has a third gene complementary for dwarf, not located.

TYPES OF GENETIC BEHAVIOR

Three general types of behavior may be noted:

1. A recessive character is expressed by a particular nullisomic in the variety. The conclusion is that only this chromosome in that variety of wheat carries the dominant allele. Double monosomics would be necessary if a second chromosome carried a dominant allele.
2. Typical gene expression - a single dose of the dominant or recessive gene as found in the monosomic (hemizygote) is sufficient for the expression of the dominant or the recessive character, respectively.
3. Genes are ineffective when hemizygous. Here the character corresponding to the recessive gene carried by the univalent is expressed only when homozygous.

(1) Recessive effect uncovered by homozygous deficiency

If a certain chromosome carries a dominant factor for a recognizable character, the corresponding nullisomic should express the effect of its absence, unless one or more of the other genomes has the same dominant factor. If all the monosomics are available for a particular variety, each nullisomic that is viable will check for the presence of any dominant genes that chromosome may carry, except as just noted. The genes for several previously known dominant characters have been identified with a particular chromosome in this manner (Sears 1953). For example, only one of the three factors for red seeds is present in Chinese. Since Chinese nullisomic 3D (16) has white seeds, this is the chromosome carrying the factor for red. Chromosome 5A (9) carried a speltoid suppressor. Several genes affecting awn expression have been located in this way, since the awnless character in Chinese is dominant. Chromosomes 4B (8) and 6B (10) in Chinese carry genes for awn suppression.

Certain Chinese monosomics when crossed with awned varieties show different degrees of awning in the monosomic offspring. The chromosomes giving this result differ for different varieties.

(2) Typical gene expression

One example of this is Unrau's results for red glume color (Unrau, 1950). The red glume color of Federation 41 segregates in a ratio of 3 red:1 white in crosses with Chinese spring. F_2's from 17 different monosomic F_1's from this cross were grown and classified. For all except monosomic 1B (1), the fits to a 3:1 F_2 ratio were satisfactory. The data are in Table 116.

Table 116. Summary of data from Monosomic F_1's from crosses of Chinese Spring x Federation 41 (White glumes x red). (Unrau, 1950, from Table 2, p. 75, Vol. 30, Scientific Agriculture).

Type of F_1	Red glumes	White glumes	Total	% White
Mono #1	528	38	566	6.7
Total of 16 other monosomics	10,975	3,462	14,437	24.0

As shown in Table 116, only 6.7% of the progeny of monosomic 1B (1) had white glumes; whereas all the other monosomics tested segregated 3:1 (only a small deficiency

of white glumed plants). Cytological examination of white-glumed F_2 plants from the monosomic 1B (1) cross showed they were nullisomic. Hence, chromosome 1B (1) carries the factor for red glumes.

The resistance of the variety Lee to race 56 of stem rust has been analyzed by the use of monosomics also (Plessers 1953). The F_2 results for the hybrid with monosomic 6 B(10) and the total of 18 other monosomics are summarized in Table 117.

Table 117. Summary of F_2 segregations for reaction to race 56 in progeny from monosomic Chinese crossed with the resistant variety Lee.

	Resistant	Susceptible	Total	% Susceptible
Monosomic 6B(10)	102	0	102	0.0
Total of 18 other monosomics	629	320	949*	33.7

* Numbers expected with 20% recombination = 626: 323.

The progeny from monosomic 6B (10) included no susceptible plants, whereas 33.7% of the progeny of 18 other monosomics were susceptible. Hence, monosomic 6B (10) carries the resistance shown by Lee to race 56. The ratio for the other monosomics is a significant deviation from 25%. It had been explained on the basis of two linked factors for resistance. The assumption of 20% recombination gives a close fit of expected to observed as shown in the Table.

Further studies have shown that the deviation is the result of a killer gene (Ki) present on chromosome 6B (10) in Chinese. It causes abortion of ki pollen in Ki ki and Ki Ki ki plants. Monosomic 6B (10) in Chinese is Ki O and has normal pollen. The ki locus is between the Sr locus in Timstein for stem rust resistance (10.5% recombination) and the Lr locus in Pawnee for leaf rust resistance (11.5% recombination) (Sears and Loegering 1961).

In addition to crosses between the variety having the character to be studied and the monosomics in Chinese, the cross with normal Chinese should be made also as a check. For the more complex characters and for those whose expression may be affected by environment, the cross with normal Chinese should be carried through F_3 to analyze satisfactorily the number of factors and the kinds of factor interaction (Burnham et al. 1955). This information is essential in interpreting the segregation in F_2 progenies from crosses with the monosomics. Knott et al. (1956) have used selfs of testcrosses to a standard variety for an analysis of the number of factors and the mode of inheritance. This should be useful when more than 2 or 3 factors are involved. It is important that the variety used in such testcrosses be recessive for the factors involved, and that the variety used as a standard in the crosses is one being used by other workers as a standard.

To identify genes whose expression is dependent on factor interaction, Sears et al. (1957) suggest that F_2 disomic lines from the cross of the monosomic with the variety be established. Since these will be homozygous for the chromosome that was a univalent in the monosomic, these lines could be used to detect interactions between that chromosome and the others. The F_2 from substitution lines crossed with the resistant variety will all be disomic for that chromosome.

(3) Genes ineffective when hemizygous

In monosomic tests for certain characters, the hemizygous condition for the re-

cessive allele (i.e. one dose in the univalent chromosome) has the same phenotype as that for the dominant allele. Only the homozygous recessive shows the recessive phenotype. This behavior will be illustrated by the sphaerococcum (s) character (Sears 1946):

	Phenotypes		Genotypes	
P_1	normal mono. 16 x sphaerococcum		SO x ss	
F_1	normal disomic,	normal monosomic	disomic	monosomic
	‖	‖	Ss	sO
			‖	‖
F_2	3 normal	3 normal	1 SS	6 OO=normal (nulli)
			2 Ss	71 sO=normal
	to	to		
	1 sphaer.	1 sphaer.	1 ss	23 ss=sphaerococcum

The expected F_2 ratios from the monosomic and the disomic F_1's are about 3:1 and seemingly no different from crosses in which the univalent did not carry the factor. The critical cross can be distinguished in F_3, since the dominant F_2 phenotypes from the monosomic F_1 plants are all monosomic and all will segregate in F_3. The nullisomics are probably recognizable as a separate class. Tests of dominant F_2's in F_3 as a regular procedure would identify the characters of this type.

Other characters that have failed to express themselves when hemizygous are Neatby's virescent, and probably the few instances in which segregation for disease reaction in F_2 of each of the crosses with the 21 monosomics did not deviate from that in the normal cross.

Production and uses of substitution lines

Sears (1953) has suggested various other uses for the monosomics in addition to that of determining which chromosomes carry particular marker genes. They may be used as tools in plant breeding for the transfer of desirable genes from one variety to another. By using them, a chromosome carrying desirable genes from one variety can be substituted for the corresponding chromosome in the variety to be improved. The complete series of substitution lines, that is 21 stocks in which a different chromosome from one variety, e.g. Kenya Farmer, has been substituted in the variety Chinese, can be used to study the contribution of each Kenya Farmer chromosome for a particular character. The reciprocal series in which each of the 21 Chinese chromosomes is in a separate stock with the 20 other Kenya Farmer chromosomes can be produced also. For this latter series, it is necessary first to transfer the monosomics to the Kenya Farmer variety, then use the aneuploids in Kenya Farmer as the recurrent parent. Two basic procedures are used in producing the necessary stocks: first, the transfer of the monosomic condition for each chromosome to another variety; second, the transfer and substitution of an intact chromosome from one variety to another.

METHODS OF TRANSFER OF THE MONOSOMIC CONDITION. The 21 monosomics were established first in the variety Chinese. As outlined by Sears (1953a) the first step in their transfer to another variety, e.g. Kenya Farmer, is to cross the 21 monosomics in Chinese as ♀ parents with that variety. The monosomic F_1's are selected and again crossed as ♀ with Kenya Farmer. The process is repeated until all the chromosomes from Chinese have been replaced by those from Kenya Farmer. Usually 5 or 6 generations should be sufficient, although the chromosome number in wheat is relatively high. The procedures may be summarized as follows, the univalent being given a superscript to indicate its source:

Description	chromosomal constitution
P_1 Chinese monosomic x Kenya Farmer	$20\ II\ Ch + I^{Ch} \times 21\ II\ K.F.$
F_1 monosomic ; disomic select discard	select $\left(\frac{20\ Ch + I^{K.F.}}{20\ K.F.}\right)$
backcross: F_1 monosomic x Kenya Farmer select monosomic, repeat the backcross	$\left(\frac{20 + I^{K.F.}}{20}\right) \times 21\ II\ K.F.$
at end monosomic is in Kenya Farmer	$\left(\frac{20\ K.F. + I^{K.F.}}{20\ K.F.}\right)$ select, backcross again

At each successive backcross, there are fewer and fewer chromosomes from Chinese, more and more from Kenya Farmer until finally all chromosomes in the monosomic are from Kenya Farmer.

Having done this for each of the 21 monosomics, the complete set has been established in Kenya Farmer. It is not even necessary that all the original set be in one variety.

Since non-disjunction for other chromosomes may occur, it is necessary to check the identity of the monosomics at the end of their transfer. One method in addition to the phenotype of the nullisomic is to cross the monosomic stock as ♀ with the mono-telocentric for that chromosome. If the univalent in the monosomic is the expected one, the mono-telo offspring should have a telocentric chromosome with no mate. If there had been a shift to a different chromosome, the telocentric would have a mate and form a heteromorphic bivalent. For example:

If the monosomic transferred to a new variety is supposed to be monosomic 8, this would be crossed as ♀ with mono telo 8. If it is 8:

	$20\ II + I^8 \times 20\ II + telo^8$		F_1's at meiosis
gametes:	21	20 + telo	20 II + ~~0~~ 0
	21	20	20 II + I
	20	20 + telo	20 II + telo *
	20	20	20 II

If it is not 8 but is 6 (i.e. lacks one 6):

	$19\ II + 1\ II^8 + I^6 \times 20\ II + telo^8$		
gametes:	21	$20 + telo^8$	20 II + ~~0~~ 0
	21	20	20 II + I
	or $19 + 1^8$	$20 + telo^8$	$19\ II + I^6 + \cancel{0}\ 0\ {}_8$*
	$19 + 1^8$	20	$19\ II + I^6 + 1^8$

* These are the critical results. If there has been a shift in the monosomic to a different chromosome the mono-telo plants from 20-chromosome ♀ gametes will have a univalent in addition to a heteromorphic pair.

The procedures in producing substitution lines will be considered next.

METHODS OF SUBSTITUTING A SPECIFIC CHROMOSOME. The methods for producing substitution lines have been discussed by Sears (1953), Unrau et al. (1956) and have been used by workers at several laboratories, Snyder et al. at Minn., Larson, Jenkins and Knott in Canada.

Three methods of substitution will be outlined, using as an example the transfer of a chromosome from Kenya Farmer into Chinese.

Method 1. The use of nullisomic Chinese as the recurrent ♀ backcross parent. The nullisomic stock is crossed with Kenya Farmer ♂. All the F_1's should be monosomic, the univalent chromosome having come from Kenya Farmer. As noted earlier, double monosomics may occur also. The F_1's are backcrossed as the ♂ parent on the same nullisomic Chinese stock. In each generation monosomic plants are selected and again backcrossed on the same nullisomic stock. At the end of the desired number of backcrosses, the monosomic plants are selfed, and disomic plants selected in the progeny. Since the univalent chromosome in each backcross progeny should be the original chromosome from Kenya Farmer, it should have been transferred intact with no chance for crossing over with its homologue. The steps might be diagrammed as follows, the univalent being given a superscript to indicate its source:

P_1	nulli Chinese x Kenya Farmer	20 II Ch. x 21 II K. F.	
F_1	monosomic F_1 (20 II + univalent)	$\frac{\text{20 Ch.}}{\text{20 K. F.}} + I^{K.F.}$	
backcross	nulli Chinese x (mono.)	Chinese chromosomes replace K. F.	$I^{K.F.}$ continues as univalent from K. F.
backcross	" x "		

final step: self monosomics, select disomics, disomics = 20 II Ch + 1 II K. F.

Nullisomics for all but chromosome 7B (7) and possibly 7D (21) in wheat are too low in vigor and fertility to be used for backcrossing. Hence, the method is not of general use.

Method 2. The use of monosomic Chinese as the recurrent parent. The monosomic F_1's are selected and backcrossed on monosomic Chinese. The monosomic offspring are backcrossed again on the same monosomic Chinese stock and this procedure is repeated. The final step is the same as for Method 1. Although it is hoped that the monosomic plant selected in each generation will have its univalent derived from Kenya Farmer as in the previous Method, there is the danger that an occasional n-1 pollen grain may function and produce a monosomic which has received its univalent chromosome from the Chinese parent rather than from Kenya Farmer. A possible way of avoiding this might be to self the monosomics and select disomic progeny from them after each generation of backcrossing. Then cross the disomic as ♂ on the same Chinese monosomic. This slows up the program and is hardly feasible. If the character being transferred is recognized easily and the plants being backcrossed are checked for the presence of the character, there is no problem in using successive backcrosses.

Method 3. The use of a mono-telocentric (20 II + telo) or a mono-isosomic (20 II + iso) as the recurrent female backcross parent. The mono-telocentric and the mono-isosomic plants occur occasionally among the progeny of the normal monosomics (see page 231). If available, the 21 different stocks are crossed as ♀ with the variety whose chromosomes are to be substituted. If a mono-telocentric is used, the F_1's will include monosomics (20 II + $I^{K.F.}$), and plants that have 20 II + telo + 1 K. F. The monosomic F_1 plants are selected and backcrossed on the same mono-telo stock. The procedure is repeated until

the requisite numbers of backcrosses have been made (at least five or six). Then the monosomic plants are selfed and the disomic progeny selected. These should be homozygous for the Kenya Farmer chromosome being transferred. The essential features are as follows:

P_1 20 II + telo Chinese x Kenya Farmer 20 II Ch. + telo Ch. x 21 II K. F.

F_1 20 II + telo + I; monosomic 20 II + $I^{K.F.}$ $\underbrace{\frac{20\ Ch.}{20\ K.F.} + \frac{telo\ Ch.}{I\ K.F.}}$; $\frac{20\ CH. + I^{K.F.}}{20\ K.F.}$

discarded selected discarded selected

backcross 20 II + telo Chinese x selected mono.

final steps: select monosomics, self them, $\frac{20\ Ch.}{20\ Ch.} + \frac{I^{K.F.}}{}$

select disomic offspring disomic= 20 II Ch. + 1 II K. F.

In this method, there is little danger of an undetected shift to a chromosome that is different from the one represented by the telocentric.

This is the most satisfactory all around method. A set in Chinese for all but one has been used by Snyder et al. (1958) in producing substitution lines in Chinese for chromosomes from the Kenya Farmer, Mida, and Marquis varieties.

PROBLEMS OF TRANSFER AND SUBSTITUTION OF CHROMOSOMES INVOLVED IN AN INTERCHANGE. One problem encountered at times in the transfer of the monosomic condition to another variety, and also in producing substitution lines, is that the two varieties may differ by one or more interchanges. The problems involved have been discussed by Sears (1953) and by Unrau et al. (1956).

If the chromosomes involved in the interchange have been identified, the crosses with those monosomics can be followed more carefully. If not, they would probably be identified during the course of the work. Thatcher may be used as an example of the problems. It differs from Chinese by an interchange between chromosomes 4 and 10. If Chinese is taken as a standard, then the two interchanged chromosomes in Thatcher may be designated as 4^{10} and 10^4 (4 with a piece of 10, and 10 with a piece of 4). To avoid additional confusion, the new chromosome numbering system is not used here.

Transfer. The steps in the transfer of the monosomic condition for chromosome 4 or 10 to Thatcher, and the expected results are as follows:

1. Chinese monosomic 4 x Thatcher
   the monosomic $F_1 = \frac{19\ Ch.}{19\ TH} + \frac{Ch.10}{TH\ 10^4}\ \frac{-}{TH\ 4^{10}}$ (Chains of 3)
   The chain of 3 indicates the univalent chromosome is involved in the interchange.
2. Select monosomic plants, cross as ♀ with Thatcher. Eventually, the monosomic progeny should have only Thatcher chromosomes and be either
   $\frac{10^4}{10^4} + 4^{10}$ or $\frac{4^{10}}{4^{10}} + 10^4$
   Once either was established, the constitution should continue.

Thus, two different monosomic lines would be established, whether the original Chinese line had been monosomic 4 or monosomic 10. As indicated by Unrau et al. (1956), to determine if the two lines were the same or different, the 40-chromosome offspring of an intercross between them might be examined.

If the same, these would be nullisomic plants with 20 II; if different, there would be 19 II + 10^4 + 4^{10}, a double monosomic. The 10^4 and 4^{10} monosomics in Thatcher would not be comparable with monosomics 4 or 10 in Chinese.

Substitution. In producing lines in which the interchanged chromosomes are substituted in Chinese, the monosomic offspring of the first cross between monosomic 10 (Chinese) and Thatcher should be:

$$\frac{19\ \text{Ch}}{19\ \text{Th}} + \frac{\text{Ch}\ 4}{\text{Th}\ 4^{10}} + \text{TH}\ 10^4$$

The most likely gametes to function through this F_1 as the ♂ in the next backcross on the Chinese monosomic 10 should be:

$$4^{10} + 10^4,\ \text{Ch}\ 4 + 10^4,\ \text{and Ch}\ 4 + 4^{10}$$

The monosomic progeny should be of three types:

$$\frac{19\ \text{Ch}}{19} + \frac{\text{Ch}\ 4}{4^{10}} + 10^4,\ \frac{19\ \text{Ch}}{19} + \frac{\text{Ch}\ 4}{\text{Ch}\ 4} + 10^4,\ \frac{19}{19} + \frac{\text{Ch}\ 4}{\text{Ch}\ 4} + 4^{10}$$

Each will have a chain of 3. At each successive backcross, the first type has a chance of yielding the other two types that have only one interchanged chromosome either 4^{10} or 10^4 which originated in Thatcher. These should be the types eventually established. The first one is disomic for 4, monosomic for 10. Each of the other two is trisomic for a segment of 4, monosomic for a segment of 10. The degree to which the segment of 4 comes to resemble Chinese will depend on crossing over. The only way of avoiding this would appear to be to use a double monosomic for 4 and 10 in Chinese, or better yet, a 19 II + telo^4 + telo^{10} for backcrossing. Even then, reciprocal substitution lines will not be comparable.

VARIETIES FOR WHICH MONOSOMICS OR SUBSTITUTION LINES HAVE BEEN PRODUCED. The complete set of monosomics is being transferred to the Rescue, Cadet, Red Bobs, and S-615 varieties by Larson at the Science Service Laboratory at Lethbridge, to Redman and Prelude by Peterson and Campbell at the Cereal Laboratory in Winnipeg, to Thatcher and Lemhi by Kuspira at the University of Alberta, and to Kharkov by Jenkins at the University of Manitoba; all in Canada (cf. Unrau and McGinnis 1958); and to Wichita by Heyne at Kansas. The full set of substitution lines is being established for the following varieties substituted in Chinese: Marquis, Mida, and Kenya Farmer by Snyder et al.; Thatcher, Hope, Timstein, and Red Egyptian by Sears. In addition, the series of 21 lines with a chromosome of the Apex variety substituted in S-615, of Rescue in Cadet, and of Cadet in Rescue are being established by Larson. The 21 substitution lines of Lemhi in Thatcher and the reciprocal substitutions are being produced by Kuspira.

OTHER USES OF SUBSTITUTION LINES. Substitution lines have many uses. Once established they may be increased and used subsequently to determine what each chromosome contributes in its new background. Tests against diseases would determine which, if any, of the chromosomes contribute resistance. The lines would be available for tests against diseases or insects which might appear later.

Lines that contribute resistance could be crossed with the recipient variety and with each other to determine the mode of inheritance (Sheen and Snyder 1962). The substitution line or lines selected from these crosses could be used as testers for further genetic analysis of the character in crosses with other lines.

By direct comparison of substitution lines information on additive effects should be obtainable. Intercrosses between lines should add additional information. Characters dependent on complementary action of factors could be studied only in intercrosses. Reciprocal substitution lines should furnish additional information.

Results using substitution lines for disease studies have been reported by Sears, Loegering and Rodenhiser (1957), Green et al. (1960), and Knott and Shen (1961).

The genetics of resistance of Kenya Farmer to several moderately virulent races of stem rust has been analyzed by studying the reactions of the 21 substitution lines of Kenya Farmer in Chinese. Those lines shown to be carrying a factor for resistance were crossed with Chinese and with each other and segregation studied in F_2 (Sheen and Snyder 1962). Several factors for rust resistance, previously unknown, were located. Also several other relationships were clarified.

Substitution lines of Thatcher, Hope and Timstein were used in studies of earliness, awning, lodging, plant height, kernel weight and yield (Kuspira and Unrau 1957). The number of lines significantly different from Chinese varied with the donor variety. For example, four Thatcher, 10 Hope and 14 Timstein lines had significantly higher yields than Chinese. The protein content of five of the Thatcher substitution lines was significantly higher than that of Chinese.

Monosomics in practical breeding

Since substitution lines can be produced by the use of monosomics or other aneuploids, it becomes possible to transfer a chromosome carrying a desired gene from one variety to another.

To accomplish this, however, the recipient variety, the one to be improved, must be monosomic for the chromosome which is to be replaced by one carrying the desired gene.

Since several transfers may be needed, the best procedure is to introduce the complete monosomic sets into the best commercial varieties. The method of doing this has been described above. A word of caution is needed at this point. The aneuploid used as the recurrent parent must be the exact equivalent of the variety. Enough backcrosses to ensure this are essential. In wheat, agronomic and baking tests might be made to determine if that had been accomplished.

The next steps are then the same as for the production of substitution lines, as outlined above. The monosomics may be used as in Method 2, or Method 3 may be used after establishing nullisomic plus telocentric or nullisomic plus isochromosome stocks. As an example, the steps in transferring a gene (on chromosome 7B (7)) from Kenya Farmer to Thatcher are outlined below, assuming that a stock of Thatcher is available that is nullisomic 7B (7) plus telocentric for one arm of 7B (7).

1. Cross the Thatcher nullisomic + telocentric with Kenya Farmer.
2. Backcross the monosomic from the F_1 in step 1, on the Thatcher nullisomic + telocentric.
3. Repeat the process, using the monosomic as the ♂ parent in each backcross.

At the end of the backcrossing, monosomics from the last backcross progeny are selfed and the disomic progeny selected. These should have 20 pairs of Thatcher chromosomes and should be homozygous for the 7B (7) chromosome from Kenya Farmer. Since this chromosome may have undesirable genes also, it may be advisable not only to self the monosomics in the last backcross progeny but also to cross them with Thatcher. Selection in the following generations from these latter crosses might be successful in combining the desirable genes brought in by the Kenya Farmer chromosome with those