MONOSOMIC ANALYSIS OF FERTILITY RESTORATION IN THREE RESTORER LINES OF WHEAT (*Triticum aestivum* L.) WITH *Triticum timopheevi* CYTOPLASM

By

FU-SUN YEN

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ABSTRACT

Genes conferring fertility restoration in each of the following three hexaploid restorer lines of common wheat (*Triticum aestivum*) carrying cytoplasm of *Triticum timopheevi* were located using monosomic analyses:

[(*T. timopheevi* x *Aegilops squarrosa*) x Canthatch^3] F_7,

[(*T. timopheevi* x *Ae. squarrosa*) x Dirk^3] F_6 and

[(*T. timopheevi* x *Ae. squarrosa*) x Karn^3] F_6.

Testcross data revealed that in the Dirk restorer, a major gene (Rf_1) conferring fertility restoration was carried on chromosome 1A, while a minor gene (Rf_4) was located on chromosome 7D. The restorer line of Canthatch was found to carry a major gene (Rf_2) and a minor gene (Rf_3) on chromosomes 6B and 6D respectively. Chromosomes 1A and 6B were found to carry genes for fertility restoration in the Karn restorer. Critical chromosomes carrying genes conferring fertility restoration in each of the three restorer lines were found not to be involved in translocations found in F1 plants of Rescue monosomics x restorer lines. Chromosomes 2A, 6A and 3D of Rescue appeared to carry genes which modified the degree of restoration obtained.

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INTRODUCTION

In recent years a new approach for increasing yield in wheat has been the commercial production of hybrid wheat. Since the discoveries of cytoplasmic male-sterility and an effective mechanism for fertility restoration, intensive efforts have been made toward the practical utilization of hybrid vigour in wheat. The main areas of hybrid research have concentrated largely on the interacting genetic factors donated by Triticum timopheevi Zhuk. and cultivated wheats.

Genetic studies designed to locate fertility restorer genes supplies the plant breeder with valuable information for hybrid wheat breeding. It also enables him to study the biochemical and genetic aspects of the mechanism of fertility restoration, to investigate the interrelationship between male-sterile cytoplasm and fertility restorer genes, which in turn can be applied to the study of phylogenetic relationships in Triticum and related species.

The goal of this investigation was to determine by use of monosomic analysis, the chromosomes which carry genes conferring fertility restoration on three restorer lines of wheat (Triticum aestivum L. varieties Canthatch, Dirk and Karn) possessing cytoplasm of T. timopheevi.

LITERATURE REVIEW

CYTOPLASMIC MALE-STERILITY IN WHEAT

Cytoplasmic male-sterility in wheat was first reported by Kihara in 1951 (7) who substituted the nucleus of hexaploid wheat into the cytoplasm of Aegilops caudata L.. Fukasawa (3) found that Triticum durum Desf. with Aegilops ovata L. cytoplasm showed complete male sterility. Wilson and Ross (26) reported that male sterility was due to an interaction of the nucleus of common wheat with the cytoplasm of Triticum timopheevi Zhuk. Male sterility was also obtained by substituting the nucleus of Triticum species into the cytoplasm of T. zhukovskyi Men. & Er., T. boeoticum Boiss.-type diploid wheat, T. boeoticum and T. monococcum L. by Maan and Lucken (14, 15).

FERTILITY RESTORATION IN WHEAT

Fukasawa (4) found that male-sterile T. durum and T. dicoccum Schrank plants with Aegilops ovata cytoplasm could be restored to fertility by pollinating with T. dicoccoides Körn. var. Kotschyanum. The use of sterility and fertility restoration in Aegilops-Triticum has been summarized by Fukasawa (6) and Kihara (8, 9).

Common wheats capable of restoring full fertility when crossed with sterile hybrids having Ae. caudata cytoplasm have not been found. Sterile hybrids with Ae. ovata cytoplasm

were consistently late in maturity and difficult to propagate (13).

Schmidt et al. (21) reported that complete fertility restoration was obtained in common wheat having T. timopheevi cytoplasm. Fertility restorer genes were transferred directly from T. timopheevi into a spring wheat by Wilson (25) who obtained fully fertile hybrids in a backcross progeny.

Wilson (27) reported that fertile hybrids were produced when male-sterile T. durum plants having T. timopheevi cytoplasm were pollinated by T. dicoccoides var. Kotschyanum.

Kihara and Tsunewaki (10) reported that fully fertile hybrids were obtained when male-sterile Bison plants having T. timopheevi cytoplasm were pollinated by T. spelta L. var. duhamelianum.

Oehler and Ingold (17) found that complete fertility restoration was obtained in hybrid plants involving Primepi hexaploid wheat as the male.

CYTOPLASMIC MALE STERILITY AND FERTILITY RESTORATION

Kihara (11) suggested that fertility restorer gene(s) effective in one cytoplasm, might not be effective in another. He found that T. spelta var. duhamelianum carried a gene(s) which conferred fertility restoration in T. timopheevi cytoplasm but not in Ae. caudata, Ae. ovata or in Ae. umbellulata Zhuk. cytoplasm. He proposed a one-to-one correspondence between fertility restorer genes and cytoplasmic units.

GENETIC STUDIES OF FERTILITY RESTORATION

Anderson (1) studying a restorer of T. timopheevi x Marquis3 origin, suggested that two dominant genes conferring fertility restoration were involved. One of these two genes was thought to have a relatively small effect which might require a particular microenvironment to be expressed, while the second had a relatively stronger effect. Livers (12) demonstrated that full fertility restoration could be explained on the basis of two dominant genes, Rf1 and Rf2, from the crosses of T. timopheevi x Marquis3 restorer with male-sterile Bison.

The influence of modifier genes was considered by Anderson (1) and Schmidt (22) to have an effect on fertility restoration. However, Robertson (19) and Robertson and Curtis (20) concluded that modifier genes had little or no effect on fertility restoration when present, but when absent, they prevented normal expression of restoration even in the presence of two fertility restorer genes, Rf1 and Rf2.

Robertson (19) and Robertson and Curtis (20) analysed the T. timopheevi x Marquis3 restorer by using Chinese Spring monosomics and male-sterile Bison. They concluded that chromosome 1A of the T. timopheevi x Marquis3 restorer carried one of the dominant genes conferring fertility restoration. Inconclusive data prevented the identification of the other chromosome carrying a fertility restorer gene. However,

chromosomes 2A, 6A, 1B, 6B, and 3D of Chinese Spring appeared to carry modifier genes influencing restoration.

As reported by Wilson (27), McCuistion (16) concluded that fertility restoration in a Nebraska wheat derivative was more complex than a 1-gene or 2-gene control.

Bajwa and Lucken (2) found that fertility restoration was conditioned by three gene pairs in R_1-Lee (Nebr.542437 x Lee), and two gene pairs in both R_3 (T.timopheevi x Marquis[3]) and R_4 ((T. timopheevi x Ae. squarrosa L.) x Dirk[3]).

Monosomic F_1's of Chinese Spring monosomics x three restorer lines (R_1-Lee, R_3, and R_4) were used to pollinate male-sterile Chris (24). Based on testcross data, it was concluded that fertility restorer genes were carried on chromosomes 1A and 5A of R_1-Lee, chromosomes 1A and 7D of R_3 and chromosomes 1A, 5A and 7D of R_4. Chromosome 1B had an inhibitory effect in R1-Lee and R_4 testcrosses. Critical chromosomes of R_1-Lee carrying restorer genes were detected only in Mexico and not in North Dakota.

Wilson (27) proposed that either the easy-to-restore female line carried fertility factors which were either additive or complementary to the fertility restorer genes, or conversely that the difficult-to-restore female produced inhibitory factors which tended to negate the additive nature of the fertility restoration mechanism contributed by the male. There appeared to be a third class of male-sterile line which did not fall in either of the two classes mentioned.

Wilson (27) suggested that fertility restoration was possibly due to at least three genes functioning as accumulative dominants in which RrRrRr was equal to RRRRRR; the individual genes might not necessarily contribute equally.

FERTILITY AND ENVIRONMENT

Fukasawa (5) observed the influence of environment on partially fertile plants from the crosses of male-sterile T. dicoccum with T. dicoccoides var. Kotschyanum derivatives. Schmidt (22) reported that the degree of restoration appeared to be affected by light intensity and/or duration and temperature. Wilson (27) reported that temperature probably was the most prominent environmental factor in affecting the expression of fertility restoration.

Variable expressions of fertility in the T. timopheevi derivatives resulted from different genetic-environmental interactions (27). Wilson (27) attempted to classify the environments into three categories - "shallow-sterile", "sterile" and "deeply sterile".

MATERIALS AND METHODS

The following materials were utilized in this program:

Cytoplasmic male-sterile lines (A-lines)

mst Cant. = (*T. timopheevi* x *Ae. squarrosa*) x Canthatch^{8}

mst CT244 = (*T. timopheevi* x Marquis^{3})F_4 x CT244^{6}

mst Dirk = [(*T. timopheevi* x *Ae. squarrosa*) x Dirk^{3}] F_4 x Dirk^{3}

mst Karn = [(*T. timopheevi* x *Ae. squarrosa*) x Karn^{3}] F_4 x Karn3

mst Marquis=(*T. timopheevi* x Marquis^{3})F_{10} x Marquis^{3}

Fertility restorer lines (R-lines)

R-C = [(*T. timopheevi* x *Ae. squarrosa*) x Canthatch^{3}] F7

R-D = [(*T. timopheevi* x *Ae. squarrosa*) x Dirk^{3}] F6

R-K = [(*T. timopheevi* x *Ae. squarrosa*) x Karn^{3}] F6

R-M = (*T. timopheevi* x Marquis^{3})F_{12}

Self-fertile varieties (B-lines)

Canthatch, Dirk, Karn and Marquis

Twenty-one correctly identified monosomic lines of Rescue and 20 lines of Redman (excluding 4B which was found incorrectly designated)

Chinese Spring ditelosomic series (including monotelocentric 4A)

Prior to using the monosomic lines of Rescue and Redman for purposes of chromosome identification, their true identity was first confirmed. For this purpose, monosomics of both varieties were crossed with the respective ditelosomics of Chinese Spring (including monotelocentric 4A) and Feulgen stained squashes of root-tips of F1 plants were cytologically examined. F1 plants with 40 chromosomes and a telocentric were saved for meiotic analysis. Spikes were collected and fixed in 6:3:1 Carnoy's fluid.

The three restorer lines of R-C, R-D and R-K were crossed to each of the 21 correctly identified monosomic lines and disomic line of Rescue (hereafter designated as "Rc"), using monosomic and disomic plants as the female. The monosomic and disomic F1's of each cross were then crossed to mst Cant., mst Dirk and mst CT244, mst Karn and mst Cant. respectively, each monosomic F1 plant being used as a separate bulk pollen source to pollinate the male-sterile plants. Testcross F1 plants derived from disomic "Rc" were used as controls.

An important feature of the present work was the use of A- and R-lines of the same common wheat variety for the test-cross. This reduced the chance occurrence of translocations and aneuploids which could otherwise appear in the progeny from intervarietal crosses. The Dirk and Karn restorers were also crossed with mst CT244 and mst Cant. respectively to study the possible restoration properties attributable to the male-sterile lines.

Early in the present study, translocations were observed at meiosis in hybrids involving "Rc" monosomics x R-C,R-D, R-K, and R-M. F_1 spikes from these hybrids were analysed cytologically to identify the chromosomes involved in the interchanges.

When all the F_1 plants of ms^t Karn x R-K and ms^t Marquis x R-M were found completely sterile (except for one F_1 plant of ms^t Marquis x R-M which had a fertility of 6%), testcrosses of ms^t Karn x ("Rc" monosomics x R-K) and ms^t Marquis x ("Rc" monosomics x R-M) were discontinued. Consequently, the number of testcross lines and sample size within lines were small. Eighty-eight testcross F_1 plants of ms^t Karn x ("Rc" monosomics x R-K) were grown in the greenhouse during the winter of 1967-68. The fertility of these plants was classified as either fertile, partially fertile, or sterile. Remnant seeds of ms^t Karn x ("Rc" monosomics x R-K) and testcross seeds of ms^t Marquis x ("Rc" monosomics x R-M) were sown in the field in 1968.

All F_1 and testcross F_1 seeds were threshed by hand to avoid any possible damage or admixtures. At the time of head emergence and before anthesis, all the heads of each testcross plant grown in the greenhouse, and at least two heads of each plant grown in the field were covered with glassine bags to prevent cross pollination.

Percentage seed set and anther type were used as a major

and an accessary criterion respectively, to estimate plant fertility. At maturity, seed set on the first tiller of a testcross plant was calculated by dividing the number of seeds in primary and secondary florets by the number of primary and secondary florets on each head.

The chromosome number of 233 testcross plants of mst Cant. x ("Rc" monosomic 6B x R-C) was determined by root-tip counts. At maturity, the fertility of each plant was recorded. The chromosome number and fertility of 22 plants of mst Dirk x ("Rc" monosomic 1A x R-D) and of 197 plants of mst Dirk x ("Rc" monosomic 6B x R-D) were similarly determined.

CLASSIFICATION OF FERTILE AND PARTIALLY FERTILE CLASSES

Two basic assumptions were made in the classification of segregating populations for fertility:

(a) Rescue does not have either a major or minor gene for restoration. Although the full expression of restoration by genes of the respective restorer lines is dependent upon modifier genes present in the Rescue complement, "Rc" monosomics were assumed to have little or no influence to intensify the expression of fertility restoration in the testcrosses of A-line x ("Rc" monosomics x R-line). F1 plants with the lowest fertility from the cross of A-lines with R-lines were considered as the minimum fertility of the fertile class in the testcross population grown under greenhouse conditions

at 21°C, high humidity and a 16-hour light photoperiod during the period of October to March at Winnipeg, Manitoba.

(b) Theoretically, plants having both dominant fertility restorer genes should be classified as fully fertile and the progeny should segregate in a 9(fertile): 6(partially fertile): 1(sterile) ratio. Similarly, plants having only one fertility restorer gene should be classified as partically fertile and the progeny should segregate in a 0(fertile): 3(partially fertile): 1(sterile) ratio. However, the expression of genes governing fertility restoration may be influenced by male-sterile cytoplasm, genetic background and environmental conditions. The fertile and partially fertile testcross plants could not be classified from the relationship between the fertility of the testcross F1 and the segregation ratio for fertility in each F2 line.

STATISTICAL ANALYSIS OF RESULTS

Because the expression of fertility restoration was affected greatly by temperature and other environmental conditions (27), the genetic analyses for the location of genes conferring restoration were based mainly on testcross data using the contingency X^2 test and/or X^2 test.

(a) For those testcross plants grown in the greenhouse during the period of October to March, the critical lines carrying genes conferring fertility restoration were determined

by means of contingency X^2 tests. The null hypothesis tested was that the frequencies of the different classes of fertility in each testcross line and the check were alike. The efficiency of a contingency X^2 test depends on the deviation of various classes of fertility from the check and true frequency of the population.

The frequency of various classes of fertility in each testcross line was also tested by a X^2 test. The purposes of a X^2 test were not only to confirm the result obtained from a contingency X^2 test, but also to classify a critical line carrying either a major or a minor gene governing fertility restoration. Individual X^2 values were calculated for each line to fit a 1(fertile): 2(partially fertile): 1(sterile) ratio which would be expected if the monosome did not carry a gene for fertility restoration. Those lines which did not fit a 1:2:1 ratio because of a deficiency of sterile plants were tested for a fit to a ratio of 48(fertile): 50(partially fertile): 2(sterile) ratio which would be expected if the critical monosome carried a gene for restoration.

(b) For those testcross plants grown under a sub-optimal environmental conditions (March to September), the critical lines carrying genes conferring fertility restoration were determined by means of contingency X^2 tests.

ASSUMPTIONS

Based on the present study, each restorer line of R-C, R-D, R-K, and R-M was assumed to carry two dominant fertility restorer genes in the homozygous condition, thus having the genotype $Rf_xRf_xRf_yRf_y$. Rescue was assumed to be homozygous recessive for these genes, or $rf_xrf_xrf_yrf_y$ (Table I).

Table 1. Expected genotypes of F_1 plants from the crosses of "Rc" monosomics x R-line.

"Rc" monosomics
$rf_xrf_xrf_y-$
$rf_x - rf_yrf_y$
$rf_xrf_xrf_yrf_y -$

x

R-line
$Rf_xRf_xRf_yRf_y$

↓

♀ \ ♂	Rf_xRf_y	Chromosome number	Remarks
rf_xrf_y	$Rf_xrf_xRf_yrf_y$	42	discard
rf_x -	$Rf_xrf_xRf_y$ -	41	critical line*
- rf_y	Rf_x - Rf_yrf_y	41	critical line*
rf_xrf_y -	$Rf_xrf_xRf_yrf_y$-	41	non-critical lines**

* chromosome carries fertility restorer gene.
** chromosomes do not carry fertility restorer gene.

Sears (23) found that the male transmission rate of n-1 gametes in wheat was 4%. Therefore, on this assumption, the theoretical ratio of 48(fertile): 50(partially fertile): 2(sterile) was expected in critical lines (Table 2). Similarly, in non-critical lines, assuming that the distribution of n-1 gametes in the four different genotypes was equal, a ratio of

1:2:1 of fertile, partially fertile and sterile plants respectively was expected (Table 3).

The difference between expected fertility ratios of critical and non-critical lines is due to the presence or absence of the chromosome carrying the recessive fertility restorer gene.

Table 2. Expected genotypes and fertility ratio of critical line for Rf_x*.

A-line rfxrfxrfyrfy x ("Rc" monosomics x R-line) Rfx - Rfyrfy

♀ \ ♂	RfxRfy 48%	Rfxrfy 48%	- Rfy 2%	- rfy 2%
rfxrfy	Rfxrfx Rfyrfy	Rfxrfx rfyrfy	rfx - Rfyrfy	rfx - rfyrfy
Fertility ratio	Fertile 48	Partially fertile 50		Sterile 2

* Similar assumptions are made for Rfy.

Table 3. Expected genotypes and fertility ratio of 19 non-critical lines.

A-line
$rf_x rf_x rf_y rf_y$ x ("Rc" monosomics x R-line)
$Rf_x rf_x Rf_y rf_y$ -

♀ \ ♂	$Rf_x Rf_y$ 24%	$Rf_x Rf_y$- 1%	$Rf_x rf_y$ 24%	$Rf_x rf_y$- 1%	$rf_x Rf_y$ 24%	$rf_x Rf_y$- 1%	$rf_x rf_y$ 24%	$rf_x rf_y$- 1%
$rf_x rf_y$	$Rf_x rf_x$ $Rf_y rf_y$	$Rf_x rf_x$- $Rf_y rf_y$	$Rf_x rf_x$ $rf_y rf_y$	$Rf_x rf_x$- $rf_y rf_y$	$rf_x rf_x$ $Rf_y rf_y$	$rf_x rf_x$- $Rf_y rf_y$	$rf_x rf_x$ $rf_y rf_y$	$rf_x rf_x$- $rf_y rf_y$
Fertility ratio	Fertile 1		Partially fertile 2				Sterile 1	

RESULTS AND DISCUSSION

CONFIRMATION OF 21 MONOSOMIC LINES OF RESCUE AND REDMAN

(i) Rescue monosomics

The spikes of F1 plants of "Rc" monosomics x Chinese Spring ditelosomics (Figure 1) with $40+1^{telocentric}$ (Figure 2) were analysed at metaphase I of meiosis and the results are presented in Table 4. A meiotic configuration of $20^{II}+1^{telocentric}$ (Figure 3) or $18^{II}+1\odot^{IV}+1^{telocentric}$ (Figure 4) indicated that a monosomic line was correctly identified. On the other hand, a configuration of $19^{II}+1^{heteromorphic\ bivalent}+1^{I}$ or $17^{II}+1\odot^{IV}+1^{heteromorphic\ bivalent}+1^{I}$ (Figure 5) indicated that univalent shift (18) had taken place and the line was incorrectly designated. One or two quadrivalents were observed in the meiotic cells of F1 plants. Only those cells are reported in which the chromosome configuration was clear. Consequently, the number of cells recorded was small. Based on the meiotic data of 26 lines, five monosomic lines of Rescue, viz., 2A(II), 3B, 4B, 5B and 2D were found to be incorrectly designated, an observation confirmed by Dr. R. I. Larson (personal communication). New Rescue monosomics 2A(II)(3 doses), 3B, 4B(5 doses), 5B(6 doses) and 2D(3 doses) were found to be correctly designated.

Figure 1. Mitotic metaphase of Chinese Spring ditelosomic 1D with 40+2telocentrics (arrows) (X 1910).

Figure 2. Mitotic metaphase of F_1 plant with 40+1telocentric (arrow) from the cross of "Rc" monosomic 6A x Chinese Spring ditelosomic 6A (X 1910).

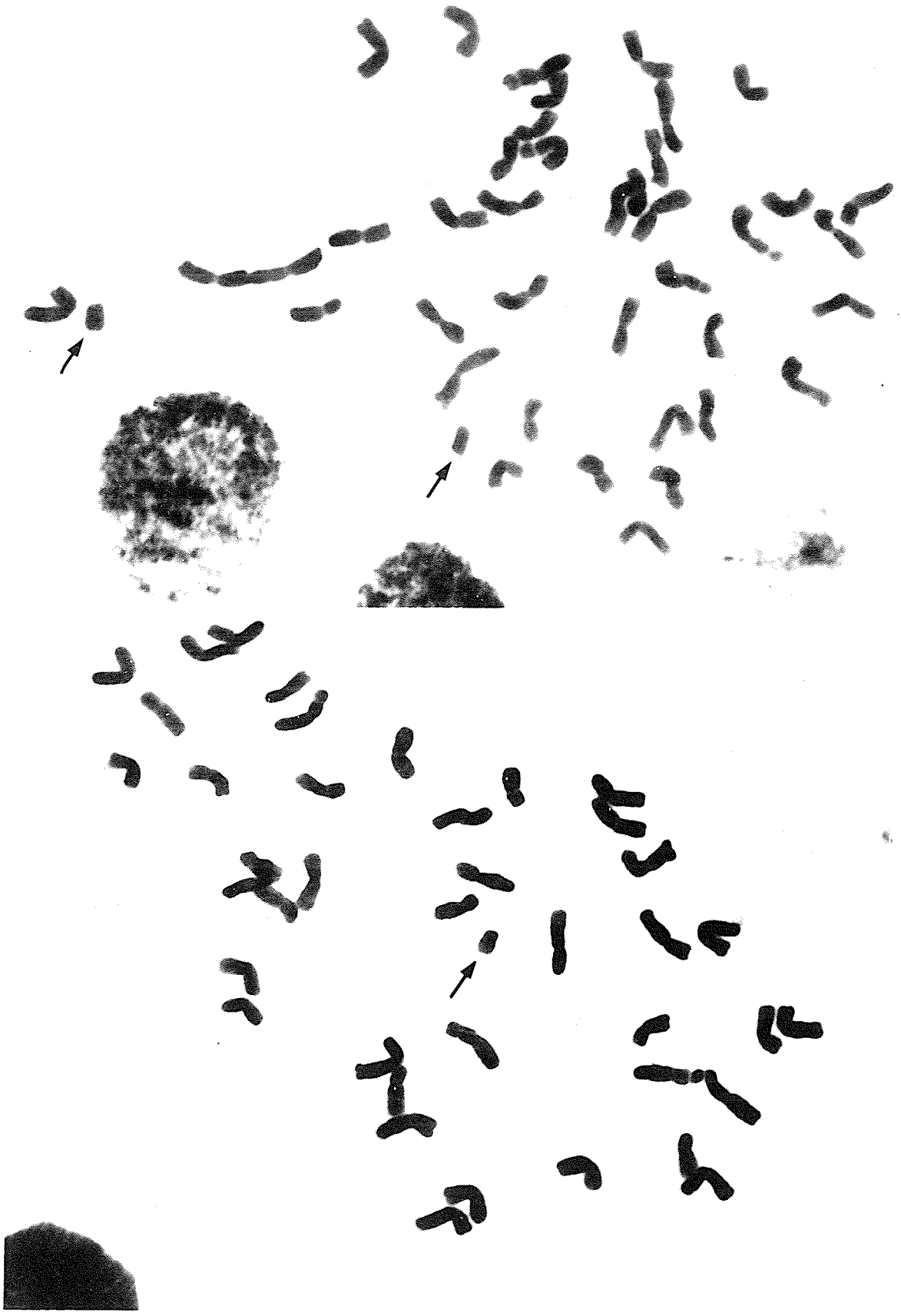


Table 4. Metaphase I chromosome configurations of F_1 plants of $40+1^{telocentric}$ constitution from crosses between "Rc" monosomics x Chinese Spring ditelosomics (including monotelocentric 4A).

Line	20^{II+1t}* and $19^{II+2I+1t}$ and $18^{II+4I+1t}$	19^{II+1H}** $^{+1I}$ and $18^{II+1H+3I}$	$17^{II+1IV\#+1H+1I}$	$18^{II+1IV+1t}$ and $17^{II+1IV+2I+1t}$	$16^{II+2IV+1t}$	Number of cells counted
1A	15			14	1	30
2A(II)		6				6
new 2A	32					32
3A	22			8		30
4A	46					46
5A	15			14		29
6A	26			5		31
7A	43			6		49
1B	7			20		27
2B(XIII)	35					35
3B		37	2			39
new 3B	41			13	2	56
4B		9	3			12
new 4B	99			90		189
5B		28				28
new 5B	5			10		15
6B	18			2		20
7B	16			7		23
1D	34			4		38
2D		20	2			22
new 2D	31			1		32
3D	18			10		28
4D	17			7		24
5D	5			14		19
6D	23			1		24
7D	24			23		47
Total						931

* t = telocentric
** H = heteromorphic bivalent
\# IV = quadrivalent (open or closed associations of 4)

Figure 3. Meiotic configuration of $20^{II}{}_{+1}{}^{telocentric}$ (arrow) of F_1 plant from cross between Rescue monosomic 7D x Chinese Spring ditelosomic 7D (X 1910).

Figure 4. Meiotic configuration of $18^{II}{}_{+1}\odot{}^{IV}{}_{+1}{}^{telocentric}$ (arrow) of F_1 plant from cross between Rescue monosomic 3D x Chinese Spring ditelosomic 3D (X 1910).

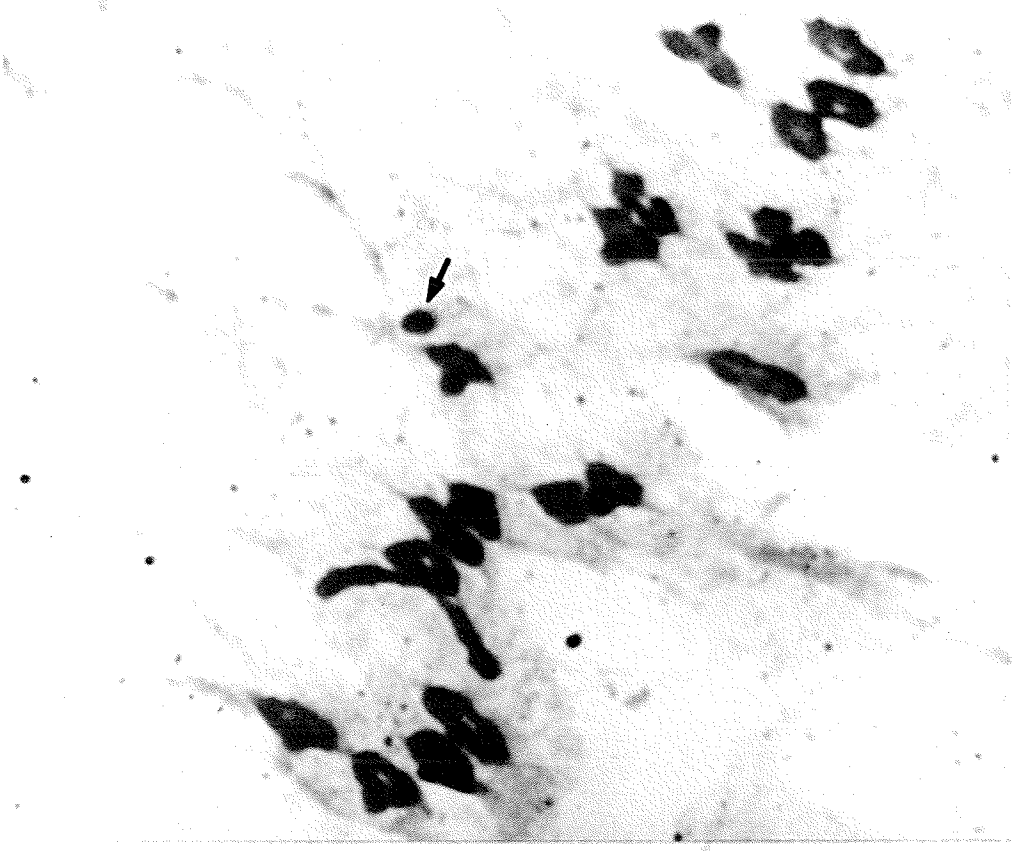


Figure 5. Meiotic configuration of $17^{II}+1\odot^{IV}+1$ heteromorphic bivalent (arrow) $+1^{I}$ of F_1 plant from cross between Rescue mono. 3B x Chinese Spring ditelosomic 3B (X 3820).

(ii) Results of metaphase counts on pollen mother cells of F_1 plants with $40+1^{telocentric}$ from crosses of Redman monosomics x Chinese Spring ditelosomics are given in Table 5. The results indicated that Redman monosomic 4B was incorrectly designated (Figure 6), while the remaining 20 lines were properly designated (Figure 7).

CHROMOSOME CONSTITUTION OF PARENTAL LINES

The chromosome number of all plants randomly taken from A-, B-, and R-lines was found to be 2n=42, a normal complement (Table 6). However, ten plants from a fully fertile F_3 line of (*T. timopheevi* x Marquis[3]) x Bison which were shown to possess two dominant genes conferring fertility restoration by Livers (personal communication) were also examined cytologically and were found to range from a chromosome number of 2n=40 to 2n=42 (Table 6). The phenotypes of these plants are shown in Figure 8.

INHERITANCE OF GENES FOR FERTILITY RESTORATION

F_1 plants from crosses between A-lines (male-steriles) and their respective fertile parental counterparts were completely sterile (Table 7). This indicated that normal varieties as pollen parents failed to impart fertility restoration to corresponding male-sterile cytoplasm.

Table 5. Metaphase I chromosome configurations of F_1 plants of 40+1 telocentric constitution from crosses between Redman monosomics x Chinese Spring ditelosomics (including monotelocentric 4A).

Line	$20^{II}+1^{t*}$ and $19^{II}+2^{I}+1^{t}$ and $18^{II}+4^{I}+1^{t}$	$19^{II}+1^{H**}+1^{I}$ and $18^{II}+1^{H}+3^{I}$	$18^{II}+1^{IV\#}+1^{t}$	Number of cells counted
1A	23			23
2A(II)	32			32
3A	13		1	14
4A	45			45
5A	22			22
6A	39			39
7A	64			64
1B	34			34
2B(XIII)	15			15
3B	18		1	19
4B		46		46
5B	37			37
6B	50			50
7B	20			20
1D	19			19
2D	67			67
3D	18			18
4D	60			60
5D	32			32
6D	46			46
7D	28			28
Totals				730

* t = telocentric
** H = heteromorphic bivalent
\# IV= quadrivalent (open or closed association of 4)

Figure 6. Meiotic configuration of $19^{II}{}_{+1}$heteromorphic bivalent$_{(arrow)}{}_{+1}{}^{I}$ of F_1 plant from the cross of Redman mono.4B x Chinese Spring ditelosomic 4B (X 1800).

Figure 7. Meiotic configuration of $20^{II}{}_{+1}$telocentric (arrow) of F_1 plant from the cross of Redman mono. 1D x Chinese Spring ditelosomic 1D (X 1800).

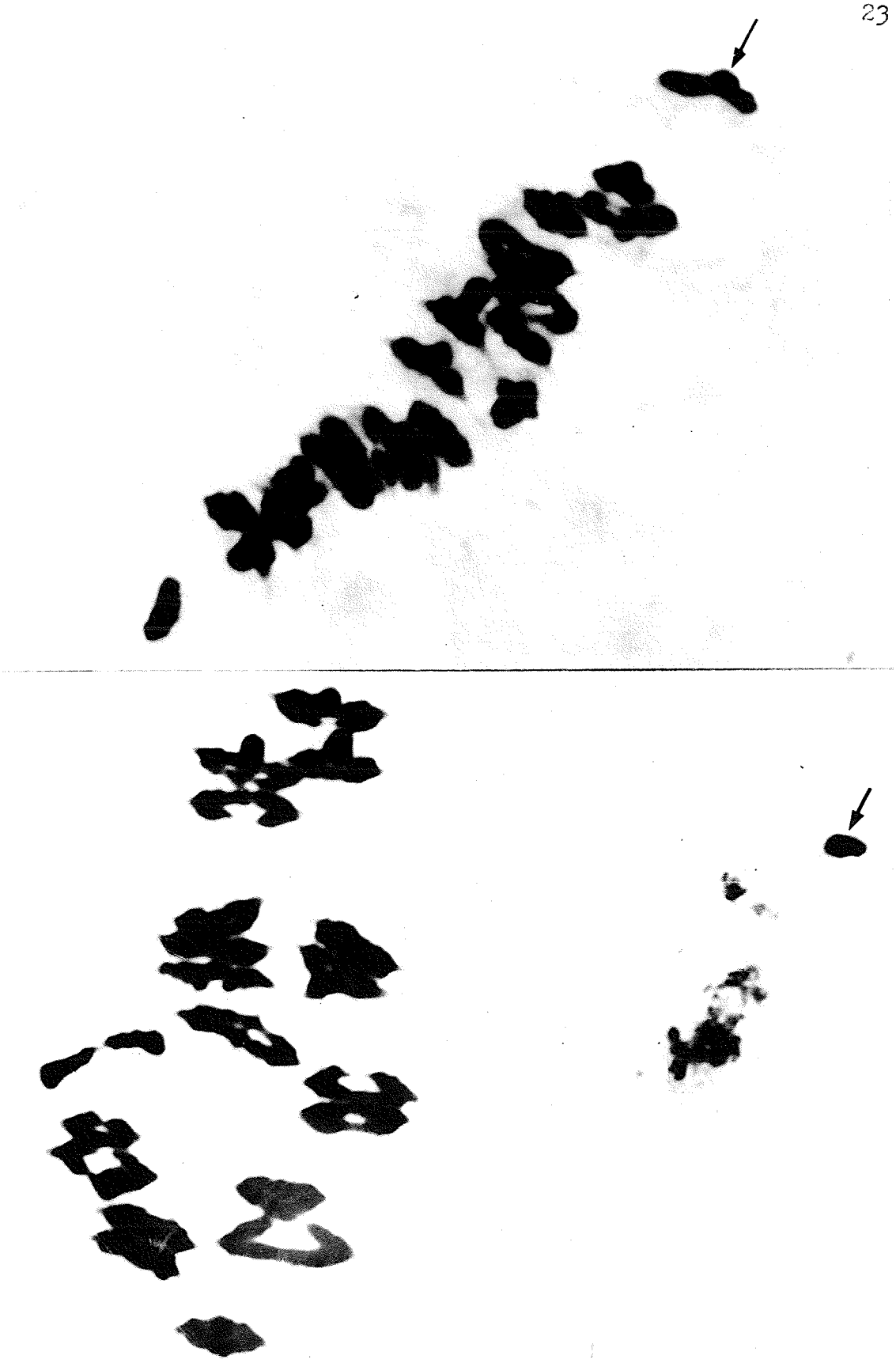


Table 6. Chromosome constitution of parental lines and F3 plants of (*T. timopheevi* x Marquis3) x Bison.

Parental line or F3 line	Number of seedlings counted		
	Chromosome number		
	42	41	40
normal Canthatch	4		
normal Dirk	4		
normal Karn	4		
normal Marquis	4		
normal CT244	4		
mst Canthatch	39		
mst Dirk	16		
mst Karn	14		
mst Marquis	14		
mst CT244	4		
R-C	7		
R-D	10		
R-K	10		
R-M	6		
(*T. timopheevi* x Marquis3) x Bison F3	3	4	3

Figure 8. 42, 41, and 40-chromosome F_3 plants of (*T. timopheevi* x Marquis^3) x Bison

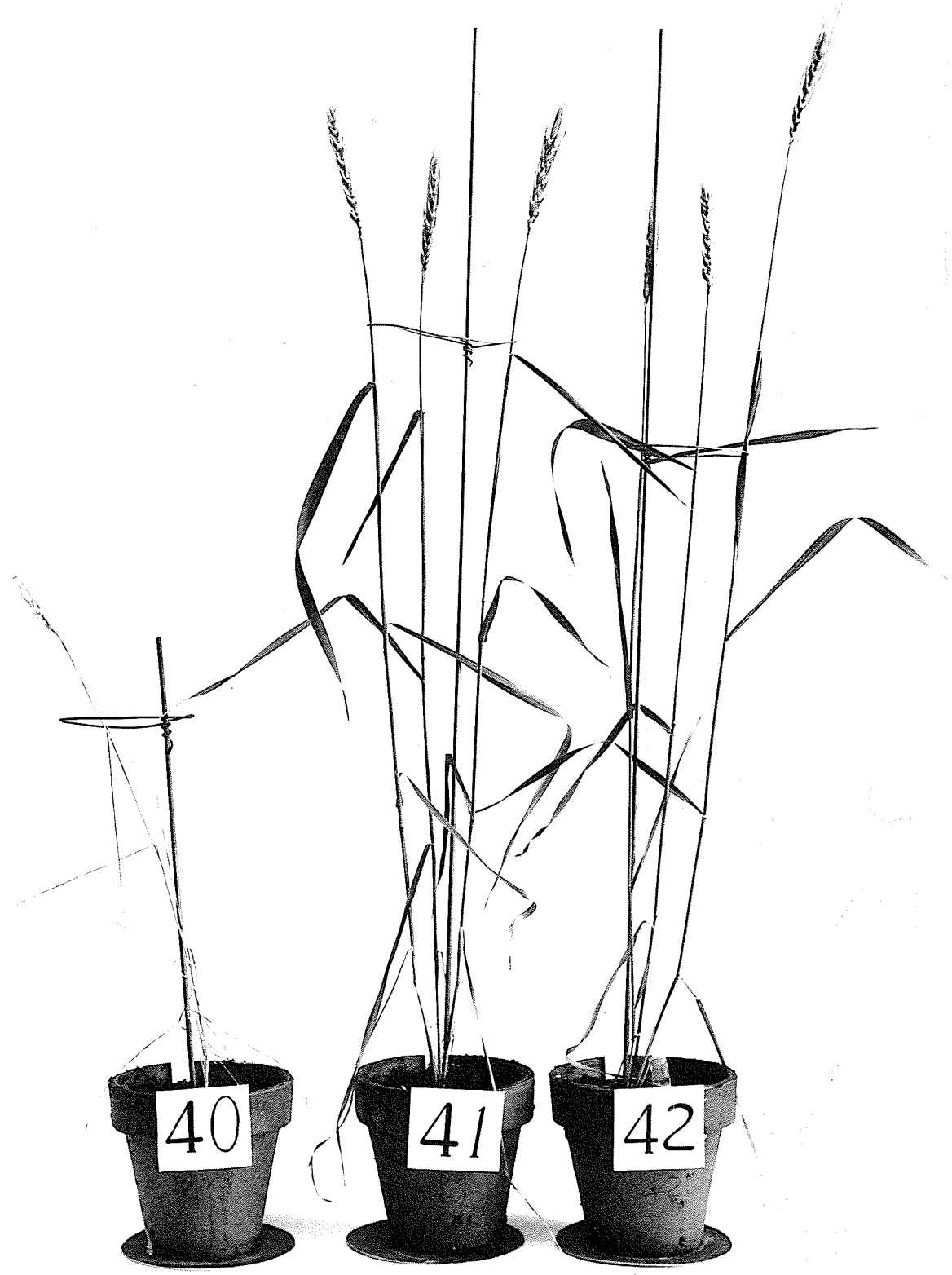

40
41
42

Table 7. Fertility of F_1 plants from various parental combinations used in the present study.

♀ \ ♂	Rescue 71-92%* 84.4** (8)#	Canthatch 64-93% 81.3 (29)	Dirk 73-97% 84.6 (20)	Karn 74-93% 86.6 (15)	Marquis 78-88% 84 (3)	Redman	Canthatch restorer	Dirk restorer	Karn restorer	(*T. timopheevi* x Marquis3) restorer
ms^t Cant.	0 (11)	0 (30)	0 (3)	0 (5)	0 (13)	0 (5)	73.5-84% (21)	81-89% (10)	86-90% (4)	0 (5)
ms^t Dirk	0 (15)		0 (30)					85-94%:0% (18)(17)		
mst Karn	0 (15)			0 (15)					0 (8)	
ms^t Marquis	0 (5)				0 (30)					6% : 0% (1)(14)
mst CT244	0 (13)			dwarf:0 (16)(2)	dwarf (8)	dwarf (3)	80-85% (2)	85-100% (17)		70-94% (19)
Canthatch restorer	73-83% 78.9 (7)	74-85% 78.1 (12)								
Dirk restorer	41-50% 45.5 (10)		99-100% 99.7 (58)							
Karn restorer	84-94% 89.4 (22)			63-100% 83.5 (92)						
(*T. timopheevi* x Marquis3) restorer	89-97% 94.9 (17)				70-83% 74.8 (9)					

* range of fertility
** average fertility in percentage
\# number of F_1 plants

As shown previously, the F1 genotype from a cross A-line x R-line may be expressed as RfxrfxRfyrfy. When these F1 plants are grown under a favorable environment, both genes should be expressed by the occurrence of complete fertility. By the same token, a plant carrying only one fertility restorer gene would be partially fertile. The F2 progeny derived from fully fertile F1 plants should segregate in a ratio of 9(fertile): 6(partially fertile): 1(sterile).

In the present study, the fertility of F1 plants of mst Cant. x R-C ranged from 73.5% to 84% (Table 7, Figure 9). In the testcross of mst Cant. x ("Rc" monosomics x R-C) hybrids with a minimum fertility level of 74% were classified as fully fertile. On this basis, segregation for fertility in all four lines of mst Cant. x R-C approximated the expected ratio of 9:6:1 as did the pooled results (Table 8). These data supported the hypothesis that fully fertile F1 plants of mst Cant. x R-C carried two dominant genes conferring restoration.

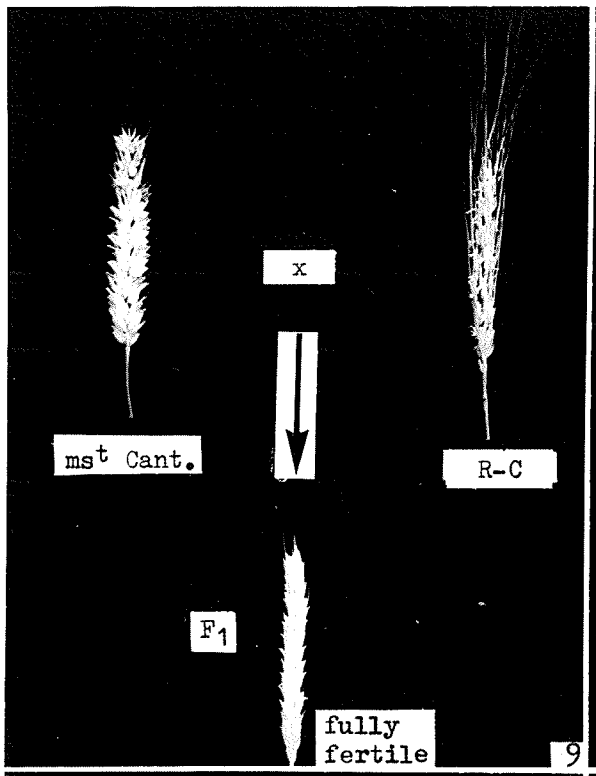
As shown in Table 7, the minimum fertility of the F1 hybrids of mst Dirk x R-D, also mst CT244 x R-D was 85%. This value was used to represent the minimum fertility level in the classification of segregating populations from both of the testcrosses, mst Dirk x ("Rc" monosomics x R-D) and mst CT244 x ("Rc" monosomics x R-D). In contrast, the fertility of F1 plants from crosses of mst Cant. x R-M, mst Karn x R-K and mst Marquis x R-M was 0%, with the exception of

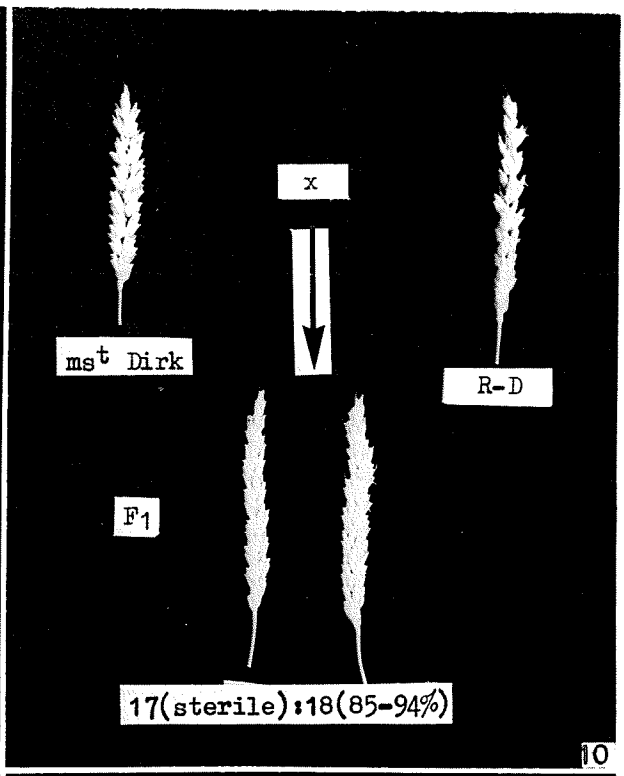
Figure 9. Spike shape of fertile F_1 plant from the cross of ms^t Cant. x R-C.

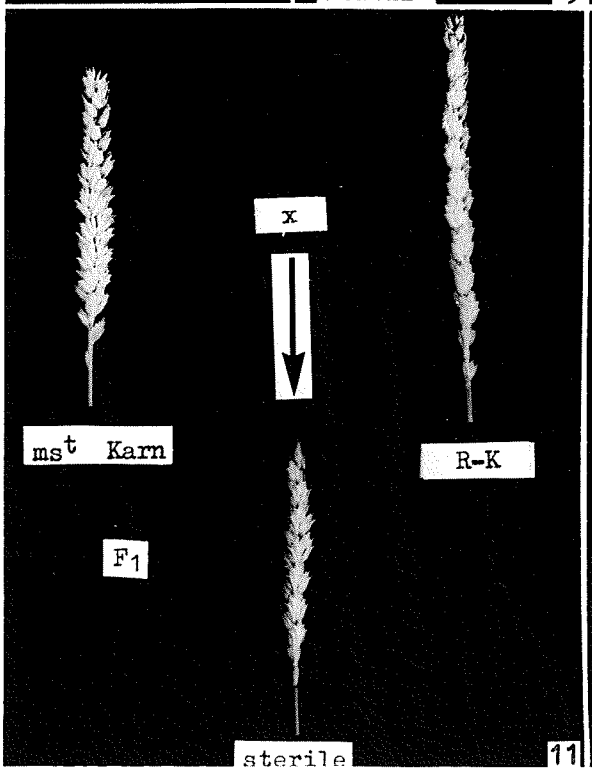
Figure 10. Spike shapes of F_1 plants from the cross of ms^t Dirk x R-D.

Figure 11. Spike shape of sterile F_1 plant from the cross of ms^t Karn x R-K.

Figure 12. Spike shapes of F_1 plants from the cross of ms^t Marquis x R-M.


x
ms^t Cant.
R-C
F$_1$
fully fertile
9


x
ms^t Dirk
R-D
F$_1$
17(sterile):18(85-94%)
10


x
ms^t Karn
R-K
F$_1$
sterile
11

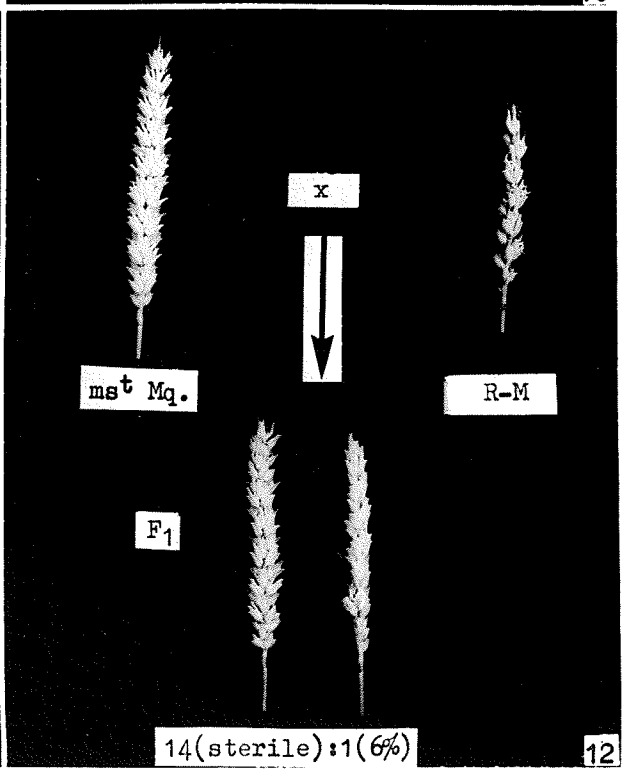

x
ms^t Mq.
R-M
F$_1$
14(sterile):1(6%)
12

Table 8. Segregation for plant fertility in progeny of cross mst Cant. x R-C, greenhouse, Oct.-Mar., 1967-68.

Fertility of F_1 plants	Total number of F_2 plants	Number of F_2 plants			X^2 value (9:6:1)	P value
		Fertile (100-74%)	Partially fertile (73-1%)	Sterile (0%)		
76%	16	8	7	1	0.28	.75-.90
78%	15	6	9	0	3.68	.10-.25
84%	18	14	4	0	3.73	.10-.25
88%	17	9	8	0	1.50	.25-.50
Totals	66	37	28	1	2.79	.10-.25

one F1 plant of mst Marquis x R-M which had a fertility of 6% (Table 7, Figures 11 and 12).

The inheritance of fertility restoration in R-D, R-K and R-M was shown to be digenic and dominant (Tables 9 and 16), as was the inheritance of restoration in R-C (Table 13).

MEIOTIC ANALYSIS OF PROGENIES OF CROSSES "Rc" MONOSOMICS X R-LINES

During the routine cytological analyses of progenies handled in this study, the presence of translocations was observed in F1 plants from crosses of "Rc" monosomics x R-C, R-D and R-K. It was recognized that the occurrence of interchanges in the progenies being classified for fertility restoration may conceivably complicate the analysis of genic restoration of fertility. Without knowledge of the degree of structural heterozygosity existing in the material, inferences made regarding genic control of fertility restoration, could be erroneous. Accordingly, 41-chromosome plants of the "Rc" monosomics x R-C (Figure 13), R-D and R-K were studied cytologically.

Meiotic configurations exhibiting a quadrivalent (e.g. $18^{II}+1\odot^{IV}+1^{I}$) indicated that the monosome was not involved in a translocation. On the other hand, the occurrence of a $19^{II}+1^{III}$ configuration was indicative that an interchange involving the particular monosome had taken place.

Table 9. Backcross F_1 data tested for a fit to a 1(fertile): 2(partially fertile): 1(sterile) or a 3(fertile + partially fertile): 1(sterile) ratio, greenhouse, Oct.-Mar., 1966-67.

Backcross	Total number of plants	Number of plants			X^2 value (1:2:1)	P value
		Fertile (100-85%)	Partially fertile (84-1%)	Sterile (0%)		
R-D x Dirk[2]	171	44	86	41	.11	.90-.95
		Number of plants			X^2 value (3:1)	P value
		Fertile + Partially fertile (100-1%)		Sterile (0%)		
R-K x Karn[2]	144	112		32	.59	.25-.50
R-M x Marquis[2]	119	95		24	1.48	.10-.25

Figure 13. Mitotic metaphase of F_1 plants of 41-Chromosome constitution from a cross between "Rc" monosomic 2B x R-C (X 1800).

In Table 10, it is seen that a high frequency of $19^{II}+1^{III}$ configurations was observed in F_1 plants from crosses involving monosomic 4A (Figure 14). It was concluded that genetic analyses of fertility restoration using Rescue monosomic 4A should be viewed with caution because of the involvement of this monosome in an interchange.

Similarly, analyses of progenies from "Rc" monosomics x R-D (Table 11) and seven monosomic lines of "Rc" x R-K (Table 12) indicated that chromosomes 2B and 1D, also chromosome 1B were translocated respectively. Trivalents involving 1D were "Q-shaped" (Table 11) suggesting that the interchanged region on this chromosome was very small.

MONOSOMIC ANALYSIS OF FERTILITY RESTORATION

(1) Canthatch restorer (R-C)-

The contingency X^2 tests for 19 lines of crosses of ms^t Cant. x ("Rc" monosomics x R-C) indicated that lines 6B, 3D and 6D were highly significant and line 4A was significant. As shown in Table 13, only line 6B satisfactorily fitted a 48(fertile): 50(partially fertile): 2(sterile) ratio (P=.90-.95), indicating that chromosome 6B of R-C carried a major gene governing fertility restoration.

Table 10. Metaphase I chromosome configurations of F_1 plants of 41-chromosome constitution from crosses between "Rc" monosomics x R-C.

Line	$20^{II}+1^{I}$ and $19^{II}+3^{I}$ and $18^{II}+5^{I}$	$18^{II}+1^{IV*}+1^{I}$ and $17^{II}+1^{IV}+3^{I}$ and $16^{II}+1^{IV}+5^{I}$	$19^{II}+1^{T**}$	$18^{II}+1^{T}+2^{I}$ and $17^{II}+1^{T}+4^{I}$	Number of cells counted
1A	23	28			51
2A(3 doses)	20	18		3	41
3A	26	20		12	58
4A	56		69	16	141
5A	25	17			42
6A	23	18		2	43
7A	21	23		3	47
1B	41	28		10	79
2B(XIII)	58	38		19	115
3B	30	16		6	52
4B(5 doses)	19	9			28
5B(6 doses)	7	20			27
6B	5	20			25
7B	24	21		19	64
1D	104				104
2D(3 doses)	38	32		8	78
3D	27	29		5	61
4D	66	25			91
5D	73	31		1	105
6D	56	38		5	99
7D	8	9			17
Totals					1368

* IV= quadrivalent (open or closed associations of 4)
** T = trivalent

Figure 14. Meiotic configuration of $19^{II}+1^{III}$ (arrow) of F_1 plant from cross between Rescue monosomic 4A x R-C (X 3500).

Table 11. Metaphase I chromosome configurations of F_1 plants of 41-chromosome constitution from crosses between "Rc" monosomics x R-D (excluding 3B and 2D).

Line	$20^{II}+1^{I}$ and $19^{II}+3^{I}$ and $18^{II}+5^{I}$	$18^{II}+1^{IV*}+1^{I}$ and $17^{II}+1^{IV}+3^{I}$ and $16^{II}+1^{IV}+5^{I}$	$19^{II}+1^{T**}$	$18^{II}+1^{T}+2^{I}$ and $17^{II}+1^{T}+4^{I}$	Number of cells counted
1A	14	57		1	72
2A(3 doses)	25	9		1	35
3A	10	8			18
4A		5			5
5A	10	15			25
6A	4	12			16
7A	23	22		1	46
1B	20	15			35
2B	9		9		18
4B(5 doses)	2	6		2	10
5B(6 doses)	2	4			6
6B	11	13		1	25
7B		15			15
1D	44		3		47
3D	11	24			35
4D	28	45		1	74
5D	46	4			50
6D	4	34			38
7D	4	5		1	10
Totals					580

* IV= quadrivalent (open or closed associations of 4)
** T = trivalent

Table 12. Metaphase I chromosome configurations of F_1 plants of 41-chromosome constitution from crosses between "Rc" monosomics x R-K.

Line	$20^{II}+1^{I}$ and $19^{II}+3^{I}$ and $18^{II}+5^{I}$	$18^{II}+1^{IV*}+1^{I}$ and $17^{II}+1^{IV}+3^{I}$	$19^{II}+1^{T**}$	$18^{II}+1^{T}+2^{I}$ and $17^{II}+1^{T}+4^{I}$ and $16^{II}+1^{T}+6^{I}$	Number of cells counted
1A	8	4			12
5A	1	4			5
1B	50		1	106	157
2B	40	31		1	72
6B	15	36		1	52
3D	24	13		6	43
4D	40	8			48
Totals					389

* IV= quadrivalent (open or closed associations of 4)
** T = trivalent.

Table 13. Testcross data for fertility restoration of ms^t Cant. x ("Rc" monosomics x R-C) using both X^2 test and contingency X^2 test, greenhouse, Oct.-Mar., 1966-67-68.

Line	Total number of plants	Number of plants					Contingency X^2 test		X^2 test (1:2:1)		X^2 test (48:50:2)	
		Fertile (100-74%)	Partially fertile (73-50%	49-25%	24-1%)	Sterile (0%)	X^2 value	P value	X^2 value	P value	X^2 value	P value
1A	183	44	33	23	20	63	5.30	.25-.50	9.20*	.01-.025	986.59**	<.005
3A	180	40	39	27	27	47	.49	.95-.975	.74	.50-.75		
4A	101	44	15	11	9	22	12.13*	.01-.025	19.10**	<.005	202.80**	<.005
5A	163	35	39	22	20	47	1.30	.75-.90	1.77	.25-.50		
6A	182	38	38	21	26	59	2.86	.50-.75	5.64	.05-.10		
7A	255	70	54	31	30	70	3.12	.50-.75	2.45	.25-.50		
1B	224	58	45	28	26	67	3.40	.25-.50	3.74	.10-.25		
2B	167	50	35	19	22	41	3.08	.50-.75	2.32	.25-.50		
3B	132	24	31	22	21	34	.43	.975-.99	3.46	.10-.25		
4B	93	24	18	13	11	27	2.08	.50-.75	1.06	.50-.75		
5B	104	28	18	11	13	34	4.60	.25-.50	4.54	.10-.25		
6B	133	62	46	11	11	3	38.65**	<.005	52.41**	<.005	.13	.90-.95
7B	134	43	27	16	14	34	4.54	.25-.50	4.19	.10-.25		
1D	225	50	48	29	32	66	1.57	.75-.90	2.49	.25-.50		
3D	171	11	31	23	33	73	19.00**	<.005	45.01**	<.005	1482.19**	<.005
4D	194	38	47	30	29	50	.23	.99-.995	3.16	.10-.25		
5D	184	47	48	25	28	36	1.14	.75-.90	3.08	.10-.25	123.62**	<.005
6D	174	76	39	20	15	24	15.03**	<.005	34.97**	<.005		
7D	175	49	39	23	26	38	1.55	.75-.90	1.39	.50		
C.K.#	90	19	22	14	14	21			1.20	.50-.75		
Totals	3264											

C.K.# = ms^t Cant. x (normal Rescue x R-C)
* = significant at .05 level
** = significant at .01 level

When line 6D was tested as the critical monosome deviation from both 1:2:1 and 48:50:2 ratios was highly significant with a deficiency of sterile plants for a fit to a ratio of 1:2:1. This would suggest that 6D of R-C carried a gene which conferred a limited degree of fertility restoration to an otherwise sterile plant; such gene(s) might be regarded as minor gene(s). Anderson's results (1) indicated that one of the genes for fertility restoration in the T. timopheevi x Marquis[3] restorer might have a relatively small effect.

Segregating progenies involving line 3D had a preponderance of sterile plants when classified according to a 1:2:1 ratio. Chromosome 3D of Rescue could be considered as possibly carrying modifier gene(s). Since 20 testcross lines were analysed, it was possible that one progeny line gave a P value below .05 significant level by chance alone. Chance deviation in line 1A therefore, could not be ruled out.

The deviation from both 1:2:1 and 48:50:2 ratios in line 4A was highly significant with an excess of fertile plants distorting the fit to the 1:2:1 ratio. It is to be recalled that chromosome 4A was involved in a translocation (Table 10) which could conceivably cause the observed deviation from the expected ratio. For this reason,

the results from line 4A must be also regarded as inconclusive.

Since the period during which this study was conducted extended over several seasons of varying conditions of photoperiod and temperature, it was necessary to analyse separately those populations grown at different periods of the year. In general, F_1 testcross plants grown under sub-optimal environmental conditions (March to Sept.), produced a higher proportion of sterile plants than populations grown under optimum greenhouse conditions from Oct. to March. Under the sub-optimal conditions, the reduced fertility indicated that the gene(s) for fertility restoration was not fully expressed. It was necessary therefore, to classify and analyse segregating populations of such material by way of contingency X^2 analysis.

An analysis of 15 lines of ms^t Cant. x ("Rc" monosomics x R-C) grown in the greenhouse during April-July (sub-optimal growth period) provided support for the acceptance of the conclusions stated above regarding the fertility restoration properties of R-C. Segregation in lines 4A, 6B, and 6D deviated highly significantly from the control (Table 14). The frequencies of sterile plants in line 6B was 8.47% and in 6D, 19.08%, supporting the conclusion that these two chromosomes carried a major and a minor gene for fertility restoration respectively. Line 4A was again variable, possibly the result of the

Table 14. Testcross data for fertility restoration of ms^t Cant. x ("Rc" monosomics x R-C) using a contingency X^2 test, greenhouse, April-July, 1968.

Line	Total number of plants	Number of plants					Contingency X^2 test	
		99-74%	73-50%	49-25%	24-1%	0%	X^2 value	P value
2A (3 doses)	136	1	15	14	22	84	12.66*	.01-.025
4A	72	20	7	4	14	27	25.84**	<.005
5A	122	4	14	17	17	70	7.57	.10-.25
6A	151	4	18	19	22	88	8.68	.05-.10
1B	82	2	13	13	16	38	4.25	.25-.50
3B	106	8	19	15	21	43	2.53	.50-.75
4B (5 doses)	150	18	24	19	27	62	4.77	.25-.50
6B	236	52	75	49	40	20	112.86**	<.005
7B	190	6	21	18	38	107	6.10	.10-.25
2D (3 doses)	166	6	25	13	32	90	3.39	.25-.50
3D	44	2	5	1	4	32	10.42*	.025-.05
4D	16	1	1	4	4	6	4.62	.25-.50
5D	22		2	4	7	9	4.86	.25-.50
6D	173	21	58	27	34	33	45.72**	<.005
7D	25	1	4	6	2	12	6.3	.10-.25
C.K.#	275	19	42	27	56	131		
ms^t Cant.^{2}xR-C	77	5	21	9	17	25	8.27	.05-.10
Totals	2043							

C.K.# = ms^t Cant. x (normal Rescue x R-C)
* = significant at .05 level
** = significant at .01 level

chromosome interchange involving chromosome 4A. Chromosomes 2A and 3D of Rescue had a less pronounced effect on fertility restoration and could be considered as possibly carrying modifier genes.

The genetic constitution of the "Rc" monosomics 2A and 2D included only 3 doses (about 87.5%) of Rescue. The conclusions therefore, regarding genic control of fertility restoration in these two testcross lines might be considered unreliable due to the degree of genetic heterozygosity existing in these two monosomics. Redman monosomics 2A and 2D were also included in testcrosses to check the accuracy of segregating properties derived from respective "Rc" monosomics. A translocation was not found in F_1 plants of Redman x R-C. The testcross data from Redman monosomics supported the finding that both chromosomes 2A and 2D of R-C did not carry genes for fertility restoration (Table 15).

(2) Dirk restorer (R-D)-

(a) mst CT244 x ("Rc" monosomics x R-D)

The contingency X^2 tests for 16 testcross lines excluding 2A, 3B, 4B, 5B and 2D showed that lines 1A and 7D were significant. Segregation for fertility in line 1A satisfactorily fitted a 48:50:2 ratio although the sample size was small (Table 16). From these results, it was concluded that chromosome 1A of R-D carried a major gene for fertility restoration.

Table 15. Testcross data for fertility restoration of ms^t Cant. x (Redman monosomics 2A and 2D x R-C) using a contingency X^2 test, greenhouse, Dec.-Mar.,1967-68.

Line	Total number of plants	Number of plants					Contingency X^2 test	
		99-74%	73-50%	49-25%	24-1%	0%	X^2 value	P value
2A	83	4	16	12	19	32	6.70	.10-.25
2D	129	23	31	18	21	36	4.81	.25-.50
C.K.#	72	6	25	10	11	20		
Totals	284							

C.K.# = ms^t Cant. x (normal Redman x R-C).

Table 16. Testcross data for fertility restoration of ms^t CT244 x ("Rc" monosomics x R-D) using both X^2 test and contingency X^2 test, greenhouse, Oct.-Mar., 1966-67.

Line	Total number of plants	Number of plants: Fertile (100-85%)	Partially fertile (84-64%)	Partially fertile (63-43%)	Partially fertile (42-22%)	Partially fertile (21-1%)	Sterile (0%)	Contingency X^2 test: X^2 value	Contingency X^2 test: P value	X^2 test (1:2:1): X^2 value	X^2 test (1:2:1): P value	X^2 test (48:50:2): X^2 value	X^2 test (48:50:2): P value
1A	22	11	8	1	1	1	0	12.61*	.025-.05	11.00**	<.005	.46	.75-.90
3A	53	15	11	5	3	4	15	.89	.95-.975	.92	.50-.75		
4A	84	28	21	10	6	4	15	3.12	.50-.75	4.07	.10-.25		
5A	65	16	16	7	6	4	16	.74	.975-.99	.0154	.99-.995		
6A	48	11	8	5	3	4	17	1.53	.90-.95	2.83	.10-.25		
7A	33	10	6	4	2	1	10	.61	.975-.99	1.48	.25-.50		
1B	27	10	5	2	2	1	7	1.60	.90-.95	2.48	.25-.50		
2B	29	7	7	3	2	2	8	.39	.995	.103	.95		
6B	9	1	1	1		1	5	4.23	.50-.75	4.56	.10-.25		
7B	40	10	7	3	3	2	15	1.54	.90-.95	3.75	.10-.25		
1D	35	8	11	5	2	2	7	2.10	.75-.90	.77	.50-.75		
3D	67	16	13	7	4	4	23	.83	.975	3.27	.10-.25		
4D	40	11	8	6	2	2	11	.42	.99-.995	.40	.75-.90		
5D	76	18	17	12	4	4	21	.72	.975-.99	.29	.75-.90		
6D	35	11	6	3	2	1	12	1.53	.90-.95	3.51	.10-.25		
7D	74	26	25	10	3	4	6	12.81*	.01-.025	12.16**	<.005	17.03	<.005
C.K.#	78	20	16	10	6	4	22			.56	.75-.90		
Totals	815												

C.K.# = ms^t CT244 x (normal Rescue x R-D)
* = significant at .05 level
** = significant at .01 level

Line 7D neither fitted a 48:50:2 ratio nor a ratio of 1:2:1. The segregation for fertility in this line was highly significant from that expected on the basis of a 1:2:1 (i.e., a non-critical line), by virtue of the low number of plants in the sterile class. This suggested that 7D of R-D also carried a gene for fertility restoration but unlike the major gene on 1A, the 7D gene exerted a minor influence.

(b) mst Dirk x ("Rc" monosomics x R-D)

The contingency X^2 tests for lines 1A and 6A were highly significant (Table 17). Line 1A was characterized by a deficiency of sterile plants, a result that supported the previous conclusion that chromosome 1A of R-D carried a major gene for fertility restoration, and that the male-sterile line used in the cross (either mst Dirk or mst CT244) had no influence on the expression of this gene. There occurred however, a discrepancy in the behaviour of other lines in this combination compared to the mst CT244 x ("Rc" monosomics x R-D) testcross. Whereas the results of 7D deviated significantly from the expected ratio in the mst CT244 testcross, they were not significantly different when mst Dirk was involved. Furthermore, the results involving 6A of the mst Dirk testcross, by virtue of the high number of plants that occurred in the sterile class, suggested that 6A of

Table 17. Testcross data for fertility restoration of ms^t Dirk x ("Rc" monosomics x R-D) using a contingency X^2 test, greenhouse, April-July,1968.

Line	Total number of plants	Number of plants						Contingency X^2 test	
		100-85%	84-64%	63-43%	42-22%	21-1%	0%	X^2 value	P value
1A	179	63	51	32	13	10	10	57.43**	<.005
2A (3 doses)	166	18	28	12	10	17	81	6.24	.25-.50
3A	231	21	46	23	14	32	95	4.62	.25-.50
4A	108	20	18	10	6	11	43	3.01	.50-.75
5A	195	29	40	24	13	22	67	.95	.95-.975
6A	180	7	26	16	13	20	98	17.45**	<.005
7A	253	32	46	27	18	24	106	1.49	.90-.95
1B	125	14	23	14	10	16	48	1.57	.90-.95
2B	182	23	32	17	13	19	78	2.24	.75-.90
3B	15	2	1	2	1		9	4.84	.25-.50
4B (5 doses)	175	26	39	17	17	14	62	.77	.975-.99
5B (6 doses)	252	37	60	34	22	12	87	3.04	.50-.75
6B	238	26	46	20	21	26	99	2.69	.50-.75
7B	186	20	31	15	13	26	81	5.44	.25-.50
1D	139	7	22	24	11	12	63	9.09	.10-.25
2D (3 doses)	173	16	37	20	11	14	75	2.49	.75-.90
3D	162	23	26	10	15	18	70	5.27	.25-.50
4D	141	17	14	19	12	19	60	8.13	.10-.25
5D	201	16	46	31	18	17	73	3.19	.50-.75
6D	206	18	40	27	22	20	79	2.59	.75-.90
7D	213	36	52	31	19	28	47	8.86	.10-.25
C.K.#	135	18	29	16	11	12	49		
Totals	3855								

C.K.# = ms^t Dirk x (normal Rescue x R-D)
* = significant at .05 level
** = significant at .01 level

Rescue might carry a modifier gene(s) for fertility restoration. However, in the testcross in which CT244 was used as the male-sterile line, 6A of Rescue did not influence fertility restoration. It was concluded that although the effect of the major gene for fertility restoration on chromosome 1A of R-D was not influenced by the male-sterile line used in the testcross, the same could not be said for other gene(s) of the Dirk restorer which might have a less pronounced effect on fertility.

(3) Karn restorer (R-K)-

The contingency X^2 tests for 6B were highly significant in both mst Cant. and mst Karn testcrosses. Similarly, results from progenies involving 1A were significant (Tables 18 and 19). Both lines 1A and 6B were characterized by a deficiency of sterile plants suggesting that each of chromosomes 1A and 6B of R-K carried a gene for fertility restoration. Different male-sterile lines used in the testcrosses had no influence on the action of these two genes.

Similar to the results of 6A in R-D testcrosses, the contingency X^2 test for line 6A in the mst Karn testcross was highly significant.

(4) (T. timopheevi x Marquis3)F12 restorer (R-M)-

The fertility of F1 plants from the cross of mst Marquis x R-M was 0% with the exception of one F1 plant

Table 18. Testcross data for fertility restoration of ms^t Cant. x ("Rc" monosomics x R-K) using a contingency X^2 test, greenhouse, Feb.-May, 1967.

Line	Total number of plants	Number of plants						Contingency X^2 test	
		100-80%	79-60%	59-40%	39-20%	19-1%	0%	X^2 value	P value
1A	44	2	23	10	2		7	13.71*	.01-.025
3A	44		10	9	5	3	17	5.97	.25-.50
4A	117	24	24	21	15	5	28	6.46	.25-.50
5A	100	9	16	18	18	9	30	3.28	.50-.75
6A	41		8	5	5	2	21	8.80	.10-.25
7A	69	10	24	13	4	3	15	5.14	.25-.50
2B	103	6	26	19	13	10	29	1.02	.95-.975
6B	31	9	14	3	4		1	17.09**	<.005
7B	25	3	8	4	2	2	6	.79	.975-.99
3D	189	14	37	40	26	13	59	3.20	.50-.75
4D	77	7	26	13	4	7	20	2.35	.75-.90
5D	50	2	21	7	2	4	14	5.05	.25-.50
6D	82	6	25	12	5	6	28	2.35	.75-.90
C.K.#	54	5	14	8	6	6	15		
Totals	1026								

C.K.# = ms^t Cant. x (normal Rescue x R-K)
* = significant at .05 level.
** = significant at .01 level.

Table 19. Testcross data for fertility restoration of ms^t Karn x ("Rc" monosomics x R-K) using a contingency X^2 test, field, April-July, 1968.

Line	Total number of plants	Number of plants						Contingency X^2 test	
		100-80%	79-60%	59-40%	39-20%	19-1%	0%	X^2 value	P value
1A	121	28	40	26	11	3	13	28.90**	<.005
2A (3 doses)	97	10	27	11	9	12	28	4.73	.25-.50
3A	180	19	43	23	20	20	55	5.43	.25-.50
4A	139	21	30	27	11	8	42	8.92	.10-.25
5A	55	3	5	14	5	7	21	10.85	.05-.10
6A	189	11	26	25	22	21	84	21.50**	<.005
7A	195	21	53	25	19	28	49	4.04	.50-.75
1B	129	14	23	15	9	33	35	7.30	.10-.25
2B	12	2	3				7	10.39	.05-.10
3B	63	4	13	13	6	11	16	2.95	.50-.75
4B (5 doses)	60	6	12	7	6	15	14	3.63	.50-.75
5B (6 doses)	14	1	1	2	4	2	4	5.66	.25-.50
6B	8		1	3	4			17.21**	<.005
7B	112	12	17	22	10	25	26	3.89	.50-.75
1D	86	9	19	10	9	20	19	3.79	.50-.75
2D (3 doses)	91	10	17	19	7	19	19	2.83	.50-.75
3D	99	10	18	12	8	22	29	4.42	.25-.50
4D	7	1	3	1	1		1	3.22	.50-.75
5D	233	23	38	39	27	50	56	4.66	.25-.50
6D	82	11	16	14	11	12	18	.78	.975-.99
7D	49	9	11	9	7	7	6	3.92	.50-.75
C.K.#	200	28	40	33	20	31	48		
Totals	2236								

C.K.# = ms^t Karn x (normal Rescue x R-K)
* = significant at .05 level.
** = significant at .01 level.

which had a fertility of 6% (cf. Section Results and Discussion). A small sample of testcross plants of ms^t Marquis x ("Rc" monosomics x R-M) was grown in the field to determine whether the genes conferring restoration carried by R-M functioned in these testcrosses. Segregation for different levels of fertility and sterility was shown to occur in the progenies.

MITOTIC ANALYSES OF PROGENIES OF TESTCROSSES

The restorer lines of R-C, R-D, and R-K were the derivatives of (*T. timopheevi* x *Ae. squarrosa*) amphidiploid x Canthatch^3, Dirk^3, and Karn^3 respectively. Also, two different varieties were involved in each cross of ms^t Cant. x ("Rc" monosomics x R-C), ms^t Dirk x ("Rc" monosomics x R-D), and ms^t Karn x ("Rc" monosomics x R-K). Intervarietal crosses might increase the frequency of aneuploids which in turn could influence fertility and segregating ratios for restoration. Mitotic analysis in the testcross plants was necessary for understanding the reliability of these data. Accordingly, chromosome number and fertility of 236 plants of ms^t Cant. x ("Rc" mono. 6B x R-C) and 197 plants of ms^t Dirk x ("Rc" mono. 6B x R-D) were analysed and the results are presented in Tables 20 and 21.

Theoretically, based on the assumption of full expression of two dominant genes conferring restoration, in the non-

Table 20. Chromosome number and fertility of testcross F_1 plants of ms^t Cant. x ("Rc" mono.6BxR-C), greenhouse, April-July, 1968.

Fertility (%)	Total number of plants	Number of plants (chromosome number)					
		43	42+1$^{telo.}$	42	41+1$^{telo.}$	41	unknown
0	20	1		15		4	
1-9	19			18	1		
10-19	10			10			
20-29	25	1		22		2	
30-39	16			15	1		
40-49	19			18			1
50-59	33		1	32			
60-69	26	1		23		2	
70-79	34	1		31			2
80-89	28			28			
90-99	6			6			
Totals	236	4	1	218	2	8	3

Table 21. Chromosome number and fertility of testcross F_1 plants of ms^t Dirk x ("Rc" mono.6BxR-D), greenhouse, April-July, 1968.

Fertility (%)	Total Number of plants	Number of plants (chromosome number)					
		43	42+1 telo.	42	41+1 telo.	41	unknown
0	83	1	2	71	5	3	1
1-9	15		1	11	2		1
10-19	7			6	1		
20-29	7			5		1	1
30-39	7		1	5	1		
40-49	7	1		6			
50-59	11			9	1	1	
60-69	9			9			
70-79	15			14			1
80-89	25			24			1
90-99	11			10			1
Totals	197	2	4	170	10	5	6

critical lines, the expected frequency of sterile plants would be 25% of which only 1/25 (or 4%) would be monosomic plants (Table 3). In the critical testcross lines, the expected frequency of monosomic plants would be 4% which consisted of equal numbers of partially fertile and sterile plants (Table 2). Chromosomes 1A of R-D and 6B of R-C carried two major genes conferring restoration (Tables 13, 14, 16 and 17). One out of 22 selected plants of mst Dirk x ("Rc" monosomic 1A x R-D) was found to be monosomic and also sterile. Eight out of 233 plants of mst Cant. x ("Rc" monosomic 6B x R-C) were found to be monosomics, half of them being sterile (Table 20). Although these results agree with the expectation for a critical line, the environmental influences should also be considered. Since these testcross plants were grown under greenhouse conditions from April to July, plant fertility was decreased because the gene(s) for restoration was not fully expressed under a less favorable condition.

GENERAL DISCUSSION AND CONCLUSIONS

Three hexaploid restorer lines of Canthatch, Dirk and Karn with T. timopheevi cytoplasm were studied by monosomic analysis in an attempt to locate genes conferring fertility restoration.

The inheritance of fertility restoration in each restorer line of Canthatch, Dirk and Karn was shown to be due to two dominant genes in the homozygous condition. Bajwa and Lucken (2) also found that restoration was conditioned by two gene pairs in the (T. timopheevi x Ae. squarrosa) x Dirk^3 restorer. Two dominant genes for restoration in T. timopheevi x Marquis^3 restorer were reported by Anderson (1), Livers (12) and Bajwa and Lucken (2).

Temperature appeared to be the most prominent environmental factor affecting the expression of fertility (27). The optimum conditions for full expression of genes conferring restoration were found in testcross plants grown under greenhouse conditions of 21°C, high humidity and a 16-hour photoperiod during the period of October to March at Winnipeg, Manitoba. Wilson (27) also found that a temperature of 21°C was ideal for stigma receptivity and pollen production.

The fertility of F1 plants of A-line x R-line involving the same or different parental lines ranged from complete sterility to full fertility (Table 7). When F1 plants were backcrossed to the parental female line, the effects of the

male-sterile female line on the expression of restoration in the progeny were also found different from variety to variety. A contingency X^2 test for fertility in segregating populations of mst Cant.^{2} x R-C plants was not significantly different from those obtained from mst Cant. x (normal Rescue x R-C), the control cross (Table 14). The progeny of mst Dirk x R-D segregated in a ratio of 18(85-94%):17(0%) (Table 7, Figure 10), and was characterized by a deficiency of plants in the intermediate range of fertility. Male-sterile Dirk seemed to have an inhibitory effect on the expression of gene(s) for restoration in the Dirk restorer line. The relationship between restorer genes and male-sterile cytoplasm appeared to be specific. These results support Wilson's proposal (27) that either the easy-to-restore female line carried fertility factors which were additive or complementary to the fertility restorer genes; or conversely that the difficult-to-restore female produced inhibitory factors which tended to negate the additive nature of the fertility restoration mechanism contributed by the male. Furthermore, a major gene would exert a strong influence on fertility restoration and would less likely be affected by the male-sterile line used in the testcross. A minor gene, on the other hand, would have a less pronounced effect on restoration and its expression could be influenced by the male-sterile line used in the testcross.

The possibility that the Rescue monosomics might carry "modifier" genes which influenced the expression of fertility restoration was also illustrated in the present study. It appeared that chromosomes 2A, 6A and 3D of Rescue carried such genes.

Livers (12) was the first one to use the symbol Rf plus an arabic numeral to designate a gene governing fertility restoration. Based on the overall testcross data (Table 22), a major gene, designated Rf1, conferring restoration was carried on chromosome 1A of the Dirk restorer. Chromosome 6B of the Canthatch restorer also carried a major gene (Rf2), as well as a minor gene (Rf3) for restoration on chromosome 6D. A second minor gene for fertility restoration was found on chromosome 7D of the Dirk restorer and was designated Rf_4. A fertility restorer gene was found to be located on each of chromosomes 1A and 6B of the Karn restorer. Talaat et al. (24) found that fertility restorer genes were carried on chromosomes 1A, 5A and 7D of the Dirk restorer. However, Bajwa and Lucken (2) reported that restoration was conditioned by two gene pairs in the same Dirk restorer. The critical chromosomes carrying either a major or a minor gene for fertility restoration in the restorer lines of Canthatch, Dirk and Karn were not involved in a translocation found in F_1 plants of Rescue monosomics x restorer lines.

Table 22. Summary of overall testcross data on the location of genes conferring fertility restoration in common wheat.

Testcross	Chromosome of restorer line carrying fertility restorer gene	Rescue chromosome carrying modifier gene(s)
ms^t Cant. x ("Rc" monosomics x R-C)	6B**(Rf_2) 6D*(Rf_3)	2A 3D
ms^t CT244 x ("Rc" monosomics x R-D)	1A**(Rf_1) 7D*(Rf_4)	
ms^t Dirk x ("Rc" monosomics x R-D)	1A**(Rf_1)	6A
ms^t Karn x ("Rc" monosomics x R-K)	1A 6B	6A
ms^t Cant. x ("Rc" monosomics x R-K)	1A 6B	

** major gene
* minor gene

The gene(s) conferring fertility restoration was originally transferred to common wheat varieties from T. timopheevi, genomically AAGG. The major gene (Rf1) conferring restoration on chromosome 1A of R-D is in all probability the same gene as on 1A of R-K and T. timopheevi x Marquis[3] restorer (19, 20 and 24). The major gene (Rf2) on chromosome 6B of R-C can be identical with the gene on the same chromosome of R-K.

The expression of major, minor and modifier genes conferring fertility restoration, especially the minor and modifier genes in testcross plants, may require specific male-sterile cytoplasm, genetic background and environmental conditions.

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