CHROMOSOME BEHAVIOUR IN WHEAT MONOSOMICS

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1. INTRODUCTION

THE use of monosomics, $6x-1$ plants, for genetical studies and for the transference of desirable characteristics from related genera into the hexaploid wheats (*Triticum vulgare*) has become an important part of the cereal breeding programme. Some particular cytological studies of the monosomes (the deficient chromosomes) have been made : Sears (1939, 1944, 1952, 1952*a*), Unrau (1950), Unrau *et al.* (1950) and Morrison and Unrau (1952). As suggested in an earlier report there are several major problems requiring clarification.

The B-series of speltoid wheats as classified by Nilsson-Ehle in 1921 has been associated with the loss of one chromosome (Winge, 1924). A review of work on this strain of wheat has been given by Huskins and Sander (1949). In the Sear's monosomic series the speltoid chromosome is number nine (mono-IX). Much of the behaviour of the other monosomes has been inferred from the reported behaviour of this monosome. The project reported in this paper was undertaken with the view of comparing the meiotic behaviour of all the monosomes.

One phase that is not yet clear is the behaviour of the chromosomes in the pollen grains (P.G's.). From time to time inferences have been made that P.G's. with varying numbers of chromosomes are produced or that telocentrics or isochromosomes may be transmitted through the male gamete, but no serious attempt has been made to study this phase of development. By the use of a new technique it was possible to make an extensive record of the behaviour of the chromosomes in the P.G's.

The morphology of the various monosomes was also compared. This was done to ascertain if any homologies were present and also as an aid to identification of telocentric or fragmented chromosomes in the P.G's. or in the somatic complement of root-tips.

2. METHODS AND MATERIAL

All investigations of P.M.C's. were made from acetocarmine squashes after whole spikes were fixed in Carnoy. Root-tips were pretreated with monobromonaphthalene, fixed in 2 BD, and then prepared as Feulgen squashes. Pollen grain preparations were made using the technique outlined previously (Morrison, 1953). For studies of megasporogenesis, ovules that had been fixed in Carnoy were embedded in paraffin and stained with crystal violet. Sections were cut at 12 microns.

The 21 monosomic lines of wheat are those developed and distributed by Sears, *i.e.* monosomics of *T. vulgare* var. Chinese Spring. The chromosomes are numbered from I to XXI and the deficient monosomes abbreviated to mono-I, mono-II, etc. Mono-XIV was not available for all studies.

3. CHROMOSOME MORPHOLOGY IN *T. VULGARE*

With the exception of the satellite chromosomes I and X it was not possible to identify each of the 21 different chromosomes by

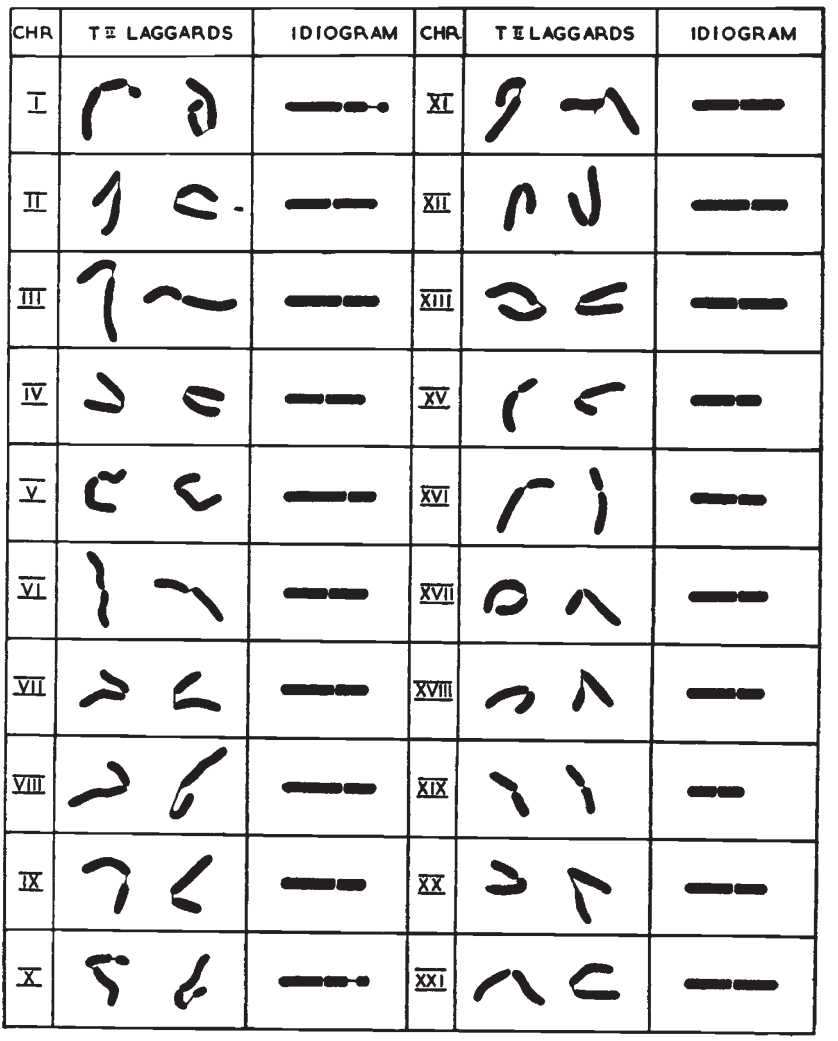

FIG. 1.—The morphology of the chromosomes of Chinese Spring; XIV is omitted. Drawings were made from univalent laggards at TII. Magnification × 1300.

morphology studies of the root-tip metaphases of the monosomics. A comparison of the chromosomes was made however from the lagging univalents at telophase II (TII). The sizes and shapes (fig. 1) agree in general with the haploid set observed in the P.G's. and with the

root-tip complement. It has long been known that IX has unequal arms. According to Sears and Camara (1952) VII is also unequal. Mono-I is sometimes visible at MI as a satellited univalent.

The methods used in the past for studying the morphology of the chromosomes have been laborious and not always fruitful. Differences in sizes are not outstanding and divergence in arm length occurs to the same degree in too many chromosomes. As well, all reports are conditioned by cytological procedures. In the earlier works (Kagawa, 1929; Bhatia, 1938; and Levitsky *et al.*, 1939) two or three constrictions per chromosome were noted. Three pairs of satellite chromosomes have been recognised by Bhatia (1938), Pathak (1939) and Camara (1944) and two pairs by Levitsky *et al.* (1939) and Tjio and Levan (1950).

At diplotene-diakinesis I have observed from one to three bivalents attached to the nucleolus. This indicates that some organising regions are weaker than others and only operate occasionally. In like manner only rarely are six nucleoli seen in a resting nucleus. The constriction in chromosome X is never visible at MI and is not constant at AII. This variability in appearance and function of the nucleolar arm may thus be an expression of the evolutionary change in this polyploid (*cf.* Darlington, 1937, p. 228 and Woods, 1937). If Larson (1952) is correct and I and X are both from one genome then the satellite chromosomes from the other genomes must be considerably changed in appearance.

From the compensating effects of tetrasomics, Sears (1952*b*) has suggested several homœologous series. The limitation of attempting a comparison by shape of chromosomes is immediately apparent in the series I, XIV, XVII. Homœologies are uncertain because of evolutionary changes.

4. MEIOSIS IN POLLEN MOTHER CELLS

Metaphase pairing.—At MI the 41 chromosomes usually form 20 bivalents and one univalent (table 1). Contrary to Sánchez-Monge and Mac Key (1948) no higher associations were found. There is no evidence for any serious degree of variation among the monosomes.

The asynaptic condition observed in four cells of mono-IX is the result of either an environmental stimulus or a mutation in the sporogenous tissue. It is not comparable to the desynapsis in nulli-III plants or to the asynapsis reported by Huskins and Hearne (1933) or Li *et al.* (1945) where all the cells within an anther showed a varying amount of failure in pairing.

Univalents at AI and TI.—At AI, the univalents may lag or they may not; they may divide or misdivide, and at TI they may be included or excluded. Frequently after division both chromatids are swept to one pole. Division of the monosome occurs in only slightly more than half of the cells. Misdivision of the centromeres

resulting in telocentrics or isochromosomes takes place in 12 per cent. of the cells (table 2). With the exception of mono-XII which is slightly low, there are no great differences among the monosomes.

TABLE 1

Chromosome pairing at metaphase I in eight monosomic lines

Monosomic	MI pairing			No. of cells examined
	$20^{II}\ 1^{I}$	$19^{II}\ 3^{I}$	$18^{II}\ 5^{I}$	
I	194	4	...	198
II	72	5	...	77
IV	385	6	...	391
VIII	88	5	3	96
IX *	161	4	...	165
XV	129	2	...	131
XVI	210	4	1	215
XIX	168	1	...	169
Total	1407	31	4	1442
Per cent.	*97·6*	*2·1*	*0·3*	...

* In another sample from this plant in which most of the cells were at interphase, there were three delayed cells at MI where pairing had completely failed. In one other cell pairing had been reduced to two bivalents and 37 univalents.

TABLE 2

Frequencies of misdivision and formation of micronuclei at interphase in eleven monosomic lines

Monosomic	Misdivision of univalents				Micronuclei in dyads	
	TI		TII			
	No. of cells examined	Per cent. with misdivision	No. of cells examined	Per cent. with misdivision	No. of cells examined	Per cent. with micronuclei
I	64	*9·4*	60	*33·3*	357	*38·9*
III	...	...	52	*27·0*	286	*40·6*
V	87	*14·9*	23	*17·4*	327	*43·1*
VIII	152	*13·8*	46	*13·0*	325	*31·7*
IX	68	*13·2*	73	*21·9*	293	*34·1*
X	120	*10·0*	28	*25·0*	534	*33·9*
XI	255	*13·3*	135	*11·1*	640	*43·9*
XII	103	*5·8*	...	...	475	*42·3*
XIII	112	*11·6*	106	*14·2*	438	*49·1*
XX	...	...	...	...	225	*53·7*
XXI	53	*17·0*	70	*11·4*	...	...
Total	1014	12·1	593	17·7	3900	41·0

The frequencies of misdivision previously reported for mono-IX are 1·7 per cent. (Sánchez-Monge and Mac Key, 1948) and 39·7 per

cent. (Sears, 1952). It is evident that different methods of scoring have been used. These workers as well reported that the univalent divided in nearly all the cells (96 and 97 per cent.) which is not in

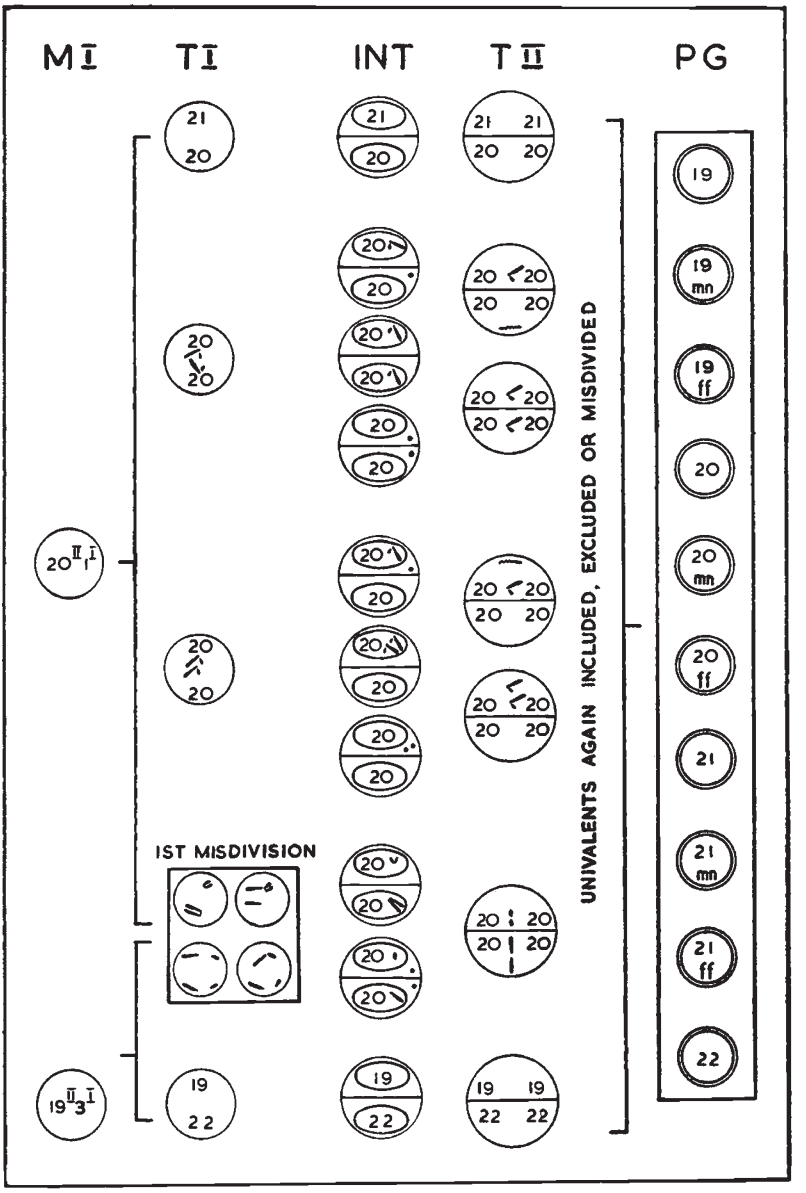

FIG. 2.—The chief variations in behaviour of the univalent chromosomes at meiosis and the resulting chromosome numbers in the P.G's. Each phase is described in the text. Micronucleus (mn) formation in the tetrads has been described previously (Morrison and Unrau, 1952).

agreement with my results. In any event misdivision frequencies cannot be estimated too accurately because of questionable phases and observations at critical times of division.

Interphase.—Univalent laggards or fragments from misdivision not included in the TI nuclei form micronuclei (table 2). One or two and less frequently three or four micronuclei per dyad were observed. There is no correlation between the frequencies of misdivision and the proportion of dyads with micronuclei among the monosomes.

There is, however, a positive correlation between the number of dyads with micronuclei and the number of tetrads with micronuclei (*cf.* Morrison and Unrau, 1952). This confirms my original assumption that the inclusion or exclusion of chromosomes from the telophase nuclei is dependent upon the specific behaviour of the univalent.

Second division.—Chromosomes at AII were counted in some cells (table 3). Actual counts were frequently limited to one sister half

TABLE 3

Distribution of the chromosomes at anaphase II

Monosomic	Anaphase II nuclei with various chromosome numbers						Total anaphase groups counted
	19	20	20+*f*	20+2*ff*	21	22	
Mono-III .	...	49	1	1	7	...	58
All others .	2	49	3	...	29	1	84
Total .	**2**	**98**	**4**	**1**	**36**	**1**	**142**
Per cent. .	*1·4*	*69·0*	*2·8*	*0·7*	*25·4*	*0·7*	...

because of non-synchronisation in both cells. In some cells the chromatids or fragments from misdivision of univalents were incorporated into the polar groups. More frequently the lagging univalents were lying between the two poles in which case they were not counted. It is impossible to tell if they will be included or excluded from the microspore nucleus. Although AII is not a satisfactory stage at which to make a great many counts or a comparison between monosomes it does given an accurate picture of the distribution of the chromosomes into microspore nuclei.

Univalent chromatids that arise through equational division at AI cannot divide again in the second division. Like the products of the delayed first division they may be included, excluded or they may misdivide. The increased misdivision at TII (table 2) will result in a general increase in telocentrics. Isochromosomes formed at first division may be separated into telocentrics. However, reunion of broken ends in the resting microspores may restore both isochromosomes and monosomes if both telocentrics are included within one nucleus.

At MII some of the micronuclei formed at the first division become

active. They behave as lagging chromatids. Other micronuclei which are isolated near the periphery of the cell are delayed in development. They have the appearance of prophase chromosomes when the others are undergoing division. They are not included in the telophase nuclei but again form micronuclei. Most of the micronuclei have disappeared from the P.G's. by the time the cytoplasm becomes vacuolated. Presumably the micronuclei are absorbed by the cytoplasm.

Whole chromosomes or fragments that are delayed in division are sometimes isolated from the tetrads as microcytes (*cf.* Frankel, 1949). These microcytes develop into small pollen grains. Although only one-eighth as large, they are similar in appearance to the normal P.G's. but have no divisions.

5. POLLEN GRAINS

Metaphase.—Although varying chromosome numbers in the P.G's. have been postulated to account for progeny results this is the first report of actual observations (table 4). The number in any P.G.

TABLE 4

Distribution of the chromosome numbers at 1st division in the P.G's. for twenty monosomic lines

Monosomic	P.G's. with various chromosome numbers											No. of P.G's. examined
	18	19		20				21		22	23	
		0*f*	1*f*	0*f*	1*f*	2*ff*	3*ff*	0*f*	1*f*			
I	...	...	...	3	1	1	...	20	...	...	...	25
II	...	...	...	31	1	1	...	16	1	...	...	50
III	...	...	...	40	2	...	...	9	...	...	...	51
IV *	...	1	1	92	5	...	...	29	...	...	...	128
V	...	1	...	8	1	...	...	18	...	...	...	28
VI	...	...	...	16	1	...	...	12	...	1	...	30
VII	1	...	...	3	...	...	...	23	1	1	...	29
VIII *	1	1	...	102	8	1	...	42	...	1	...	156
IX *	1	1	1	78	7	1	...	51	1	...	...	141
X *	...	...	...	39	4	3	...	35	...	1	1	83
XI	...	...	...	30	...	1	...	9	1	...	...	41
XII	...	...	...	34	...	...	...	5	...	...	1	40
XIII	...	...	...	35	1	1	...	34	...	...	1	72
XV *	...	1	...	48	10	...	...	16	...	...	...	75
XVI	...	1	...	21	...	...	...	3	...	...	...	25
XVII *	...	...	...	72	5	...	...	30	...	...	...	107
XVIII	...	...	...	18	2	...	...	10	...	1	...	31
XIX	1	1	...	52	6	...	...	15	...	1	...	76
XX	...	...	...	66	10	2	...	15	...	...	...	93
XXI	...	1	...	24	1	...	1	1	...	...	...	28
Total	4	8	2	812	65	11	1	393	4	6	3	1309
Per cent. of Total	0·3	0·6	0·1	62·0	5·0	0·8	0·1	30·0	0·3	0·5	0·2	

Mean number of chromosomes per P.G. = 20·3.

* Combined results for two years.

depends upon the inclusion or exclusion of lagging univalents in that particular microspore nucleus.

The 1951 results showed significant differences among the monosomes for the formation of P.G's. with 20 or 21 chromosomes. From more extensive studies in 1952 it is evident that results for the two years vary considerably (table 5) and that no specific ratio can be established from the results of the small samples.

TABLE 5

Distribution of the chromosome numbers at 1st division in the P.G's. for two years, for mono-IX and mono-X

Mono. year	P.G's. with various chromosome numbers										No. of P.G's.	No. of chrs.*	Mean per P.G.
	18	19		20			21		22	23			
		0*f*	1*f*	0*f*	1*f*	2*ff*	0*f*	1*f*					
IX-1951	...	...	...	17	2	...	22	...	...	...	41	842	20·5
IX-1952	1	1	1	61	5	1	29	1	...	...	100	2026	20·3
X-1951	...	...	...	19	3	2	7	...	1	1	33	672	20·4
X-1952	...	...	...	20	1	1	28	...	...	...	50	1028	20·6

* Omitting fragments.

Some of the apparent heterogeneity among the different monosomes may be due to differences in the stage of anther development. If the P.G's. with 20 chromosomes are sufficiently unbalanced they will be delayed in coming to mitosis. Then if the anthers are examined late in the cycle a bias in the favour of the 20-chromosome P.G's. will be introduced. No estimate of this bias could be made by counting the number of uni-nucleate and bi-nucleate P.G's. present.

Disregarding fragments and using the total for all monosomes (table 6) the ratio of the various numbers agrees with results for AII. As expected, the frequency of 18, 19, 22 and 23 is low, but these P.G's. are produced in sufficient numbers to warrant attention as possible gametic sources of variation.

Because of the loss of chromosomes as micronuclei, more P.G's. with 20 than with 21 chromosomes are expected. Even in the tetrads with no micronuclei two of the microspores will be deficient. As 50 per cent. of the tetrads have one or two micronuclei (Morrison and Unrau, 1952) the ratio of P.G's. with 21 to 20 chromosomes should be approximately 25 : 75. My results are not greatly divergent from this ratio.

Deficient chromosomes were tabulated as fragments because it was not always possible to discriminate between telocentrics and

chromosomes with ruptures near the centromere. Of all fragments, 60 per cent. were certain telocentrics, another 15 per cent. were inferred and 25 per cent. were doubtful. There is no correlation between misdivision frequencies and number of fragments observed for the various monosomes.

TABLE 6

Distribution of the chromosome numbers and a comparison of frequency of fragments at 1st division in the P.G's.

ff	P.G's. with various chromosome numbers							No. of *ff*
	18	19	20	21	22	23	No. of P.G's.	
0 . . .	4	8	812	393	6	3	1226	0
1 . . .	...	2	65	4	...	...	71	71
2 . . .	...	...	11	...	...	...	11	22
3 . . .	...	...	1	...	...	...	1	3
Total . .	**4**	**10**	**889**	**397**	**6**	**3**	**1309**	**96**
No. of cells with *ff*	...	2	77	4	...	...	**83**	...
ff per cent. .	...	*20·0*	*8·7*	*1·0*	...	...	*6·3*	...

TABLE 7

Anaphase and telophase of 1st division in P.G's. in six monosomic lines

Monosomic	Anaphase or telophase in the P.G's.		
	Normal with no laggards	With laggards	Total examined
I . . .	68	2	70
VII . .	7	1	8
VIII . .	65	1	66
XV . .	18	0	18
XX . .	34	2	36
XXI . .	65	0	65
Total . .	**257**	**6**	**263**
	97·7 per cent.	*2·3* per cent.	...

No actual isochromosomes were recorded although two probables were seen. It would be difficult to distinguish them from chromosomes with median centromeres except those duplicated for the trabant arm of I or X. In three P.G's. chromosomes deficient for only a portion of an arm were seen.

An examination of the second mitotic division showed that P.G's. with 20 and 21 chromosomes were undergoing division. Results were not tabulated because the numbers of observations were limited. The smallness of the chromosomes also prevented an accurate analysis.

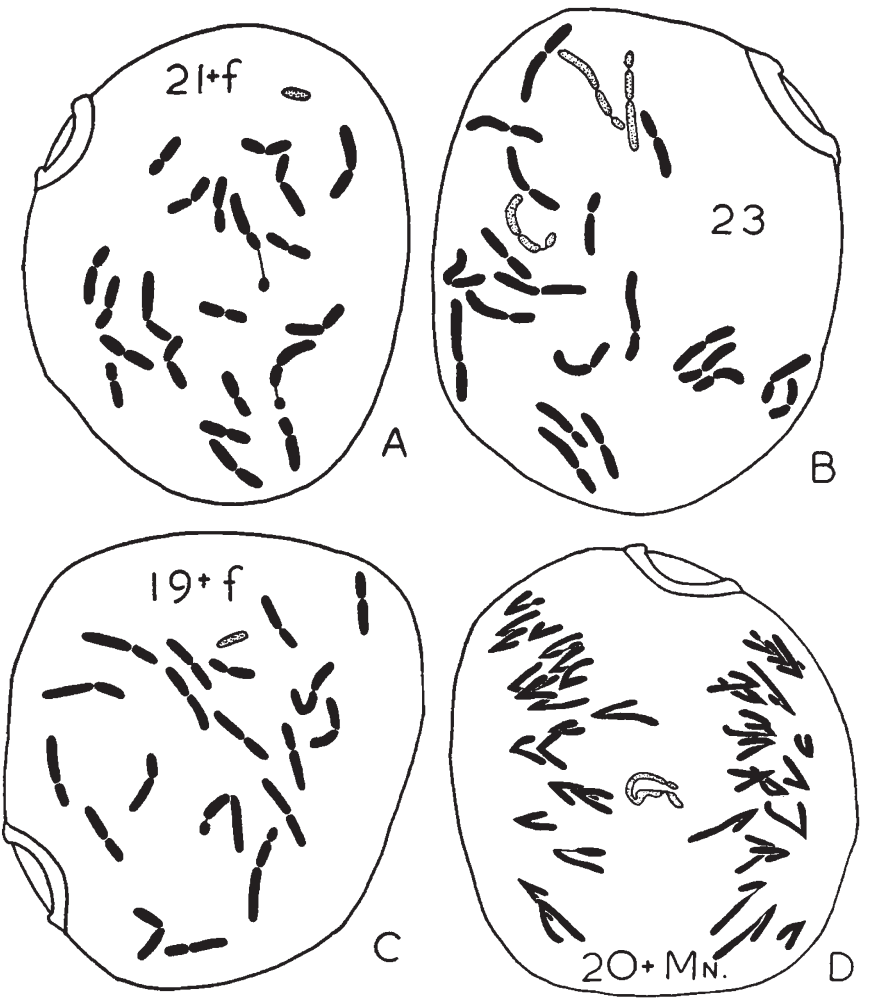

FIG. 3.—Four pollen grain mitoses, odd chromosomes stippled. The P.G. wall is not drawn to scale. Magnification × 1300.

Anaphase and Telophase.—Studies were made of anaphase and telophase in six monosomic lines (table 7). No attempt has been made to compare the various monosomes statistically because of the small numbers for some monosomes. The frequency of abnormal behaviour calculated from the total is probably near correct for all monosomes.

The six laggards can be classified into two types :—

(1) Cells with extra nuclear material out of phase. Micronuclei carried over into the P.G's. become active but are delayed

in development (fig. 3D). The action of the micronucleus is comparable to the action it frequently undergoes at interphase. The two laggards in mono-XX were of this kind.

(2) Cells with centric fragments or chromosomes that have sub-effective centromeres (some may be acentric fragments) which were included in the microspore nucleus at TII. The other four were of this kind (fig. 4J).

Darlington (1940) proposed non-disjunction of telocentrics at P.G. mitosis to account for the production of isochromosomes in *Fritillaria*. Sánchez-Monge and Mac Key (1948) have proposed a similar mechanism in wheat. No support for this theory was found. Nor is there any support for the second postulate of Rhoades (1940) whereby isochromosomes produced at meiosis become micronuclei which are carried over to the P.G. and then become active. As Sears (1952*a*) has suggested, isochromosomes and telocentrics arise directly through misdivision at meiosis.

6. MEIOSIS IN EMBRYO SAC MOTHER CELLS

Observations of meiosis were made from sectioned ovules of mono-VII, XVI, XX and XXI. The behaviour of the univalent (fig. 4D) is similar to its behaviour in the P.M.C's., *i.e.* it lags. divides and forms micronuclei, etc. The plane of division in one dyad is at right angles to the other however, and this results in a T-shaped tetrad of megaspores (fig. 4E).

The wheat gametophyte is monosporic and it is always the innermost cell (cell number 4) that develops into the embryo sac. Micronuclei are found in all four megaspores. Out of a total of 48 tetrads 79·2 per cent. had one or more micronuclei. In mono-XX out of 27 tetrads 81·5 per cent. had micronuclei.

If no micronuclei are present we cannot be certain whether the terminal megaspore or the first two have 21 chromosomes. Again, if there is one micronucleus in the third megaspore it does not indicate the deficiency or completeness of cell number four. Probably the best check on the formation of deficient or normal gametes can be made from crossing and selfing experiments. Sears (1944) has shown that in general 75 per cent. of the female gametes are deficient.

7. PROGENY

A record was kept of the chromosome number of all plants grown to maturity (table 8). Results for individual monosomics are not of sufficient magnitude to warrant a comparison. Of the total, the ratio of normal to monosomic plants is slightly higher than expected but the number of nullisomics compares favourably with previous reports (Sears, 1944 ; and Smith *et al.*, 1949).

As the amount of zygotic elimination and embryo abortion is practically nil we must assume excessive certation, partial pollen sterility at later stages or slower pollen tube growth of defective P.G's., to account for the ratio. With a ratio in the female of monosomic to normal as 75 : 25, then P.G's. with 20 chromosomes can be only one-thirtieth as efficient as the P.G's. with 21 chromosomes or there would be many more nullisomics produced.

TABLE 8

Progeny grown from monosomic seed

	Type of plant and chromosome number				Total
	Disomic 42 chromosomes	Monosomic 41 chromosomes	Nullisomic 40 chromosomes	Other Aberrants *	
No. of plants .	68	101	2	6	177
Per cent. .	*38·4*	*57·1*	*1·1*	*3·4*	...

* These plants were as follows :—

i. 1 with 40 plus an isochromosome.
ii. 2 with 41 plus an isochromosome.
iii. 2 with 41 plus a telocentric.
iv. 1 with 40 plus a telocentric plus a chromosome with an interchange that arose through fusion of telocentrics, a process to be described later.

With 6·3 per cent. of all P.G's. having fragments it is not surprising that a proportion of all progeny from selfed monosomics have either telocentrics or isochromosomes. Deficiencies can be transmitted through the egg as well. Of chief importance to the plant breeder is the phenotypic expression of small or large deficiencies or duplications which can arise through the processes of misdivision of the univalent chromosome at meiosis.

8. SUMMARY

1. The 21 expected monosomics in *T. vulgare* can be identified by crossing. Only two or three of them can be distinguished by chromosome structure.

2. In all monosomics 20 bivalents are formed in 97 per cent. of the P.M.C's. Chromosome mosaics, both hypoploid and hyperploid cells, were found in monosomic and disomic lines (see Appendix).

3. The univalents either divide or misdivide and either lag or do not lag at either first or second telophase.

4. Isochromosomes in wheat arise directly through misdivision at meiosis and not indirectly through non-disjunction in the P.G's.

5. P.G's. with 18-23 chromosomes are formed and undergo mitosis.

Six per cent. of the P.G's. contain fragments, most of which are telocentrics.

6. Over twice as many P.G's. with 20 as with 21 chromosomes are produced but the former are only 1/30th as effective as the latter in fertilisation.

APPENDIX

Chromosome mosaics at metaphase I.—At MI 32 cells with a reduced or aneuploid number and two cells with a hyperploid number were observed (table 9). Following the terminology of Sachs (1952) who found aneuploid cells in *Triticum* hybrids, these abnormalities are classed as chromosome mosaics.

Frequencies are not intended to show differences among the monosomes because in other slides from the same spikes no mosaics were found. Normally there are over 500 P.M.C's. in a squash of three anthers but because of non-synchronisation only about 300 at full MI are expected. In those slides where the number of cells at MI is small the predominating stage was telophase or interphase. Presumably the unbalanced cells are less efficient and thus are delayed.

TABLE 9

Distribution of chromosome mosaics in pollen mother cells

Plant type	Total no. of cells at MI in squash of 3 anthers	Chromosome mosaics		
		No. of aberrant cells	Chromosome no. in the aberrant cells	Pairing arrangement
DISOMICS				
A . . .	36	1	29	$8^{II}\ 13^{I}$
B . . .	43	2	29	$9^{II}\ 11^{I}$
MONOSOMICS				
I . . .	198	1	77 †	$37^{II}\ 3^{I}$
II . . .	83	6	30	$10^{II}\ 10^{I}$
VI . . .	222	3	32	$12^{II}\ 8^{I}$
VIII . . .	96	1	23	$5^{II}\ 13^{I}$
		1	16	$2^{II}\ 12^{I}$
XV . . .	200	2	19	$6^{II}\ 7^{I}$
XVII . .	73	14	32	$12^{II}\ 8^{I}$
				$11^{II}\ 10^{I}$
XVIII . .	1021 *	2	32	$12^{II}\ 8^{I}$
MONOSOMIC				
XIV+ISO−XIV	93	1	73 †	$35^{II}\ 3^{I}$

* Count from 3 florets. † Hyperploid cells.

In mono-XVII evidently the abnormality must have occurred at least four cell generations prior to meiosis. Premeiotic mitoses were examined in two plants but out of 275 cells at anaphase or metaphase no spindle irregularities were observed. There were three doubtful cells, two with a bridge and one with a micronucleus. With abnormal divisions occurring so early in the anther development it is difficult to get cytological proof. It is probable, however, that the aneuploid cells are caused by multipolar spindles as suggested by Sachs (1952). Hyperploid cells can be explained by fusion of two spindles.

Because the chromosome mosaics appeared in disomic plants it may be an indication of the instability of Chinese Spring. It may also suggest that the chromosome mosaics may be the result of either environmental stress or gene mutation and that close scrutiny would reveal their presence in other non-hybrid material. With the rare occurrence of chromosome mosaics and with the competition they would suffer it is unlikely that many aneuploid cells would form viable P.G's. However, it is a possibility. They thus may prove a source of variation for plant breeders. In any event they offer an explanation for some of the abnormal chromosome numbers reported from time to time in cereals.

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FIG. 4.—Photomicrographs of meiotic stages and mitosis in the P.G's. D and E at ×500, all others at ×1000.

A. MI in P.M.C., 20^{II} 1^{I}.

B. MI in aneuploid P.M.C. from mono-VIII, 5^{II} 13^{I}.

C. A II, one side only, from mono-III, 20 chromosomes towards each pole with the misdividing univalent between them.

D. MI in M.M.C., 20^{II} 1^{I}.

E. Late T II in M.M.C. No laggards and therefore no micronuclei formed in the megaspores.

F. P.G. mitosis, 21 chromosomes.

G. P.G. mitosis, 20 plus a telocentric chromosome, in the group at two o'clock.

H. P.G. mitosis, 20 chromosomes.

J. P.G. mitosis, anaphase from mono-VII, sub-efficient chromosome at six o'clock left. 20 chromosomes at each pole.

A
B
C
D
E
F
G
H
J

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