For Reference

NOT TO BE TAKEN FROM THIS ROOM

THE BEHAVIOR OF THE UNIVALENT CHROMOSOMES OF
MONOSOMIC TRITICUM VULGARE AT MEIOSIS

J. W. Morrison

Department of Plant Science
University of Alberta

Thesis
1951
34

*For reference: not to be
taken from this room.*

EX LIBRIS
UNIVERSITATIS
ALBERTAENSIS

Digitized by the Internet Archive
in 2017 with funding from
University of Alberta Libraries

<https://archive.org/details/behaviorofunival00jack>

T H E U N I V E R S I T Y O F A L B E R T A

THE BEHAVIOR OF THE UNIVALENT CHROMOSOMES OF
MONOSOMIC TRITICUM VULGARE AT MEIOSIS

A DISSERTATION

SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

FACULTY OF AGRICULTURE
DEPARTMENT OF PLANT SCIENCE

by

Jack William Morrison

EDMONTON, ALBERTA

APRIL, 1951

U N I V E R S I T Y O F A L B E R T A

FACULTY OF AGRICULTURE
DEPARTMENT OF PLANT SCIENCE

The undersigned hereby certify that they have read and recommend to the School of Graduate Studies for acceptance, a thesis entitled, "The Behavior of the Univalent Chromosomes of Monosomic Triticum vulgare at Meiosis", submitted by Jack William Morrison, B.Sc., in partial fulfilment of the requirements for the degree of Master of Science.

PROFESSOR

John Huron

PROFESSOR

G. H. Moss

PROFESSOR

Jack W. Morrison

Date

April 3, 1951.

ABSTRACT

This study was carried out to determine the behavior of the univalent chromosomes of Triticum vulgare* at meiosis. In particular it was made to ascertain if differences or similarities of behavior existed among any of the 21 monosomes of Chinese Spring. The two major problems studied were the division of the univalent and the formation of micronuclei by the lagging univalent.

Differences and similarities existed among the 21 monosomes in regard to the percentages of the quartets containing micronuclei. The values obtained ranged from 34.1% for Mono-X to 65.2% for Mono-II. Little variability was observed between plants within a monosomic line or between florets, spikelets, or anthers within any particular plant. It was therefore concluded that the factor (or factors) regulating the formation of micronuclei was inherent within each univalent chromosome.

* The priority of Triticum aestivum L. for the common bearded wheat species is recognized. However, T. vulgare Vill. as amended by Host has been accepted by most wheat specialists because it is more descriptive of this species.

The occurrence of micronuclei at the telo-interphase stage of division was noted. A correlation between the percentage of quartets with micronuclei and the percentage of the telo-interphase cells with micronuclei was established for some but not all of the monosomes.

Five other aberrations other than monosomics were found. Because in these plants a percentage of the quartets had micronuclei it was concluded that the presence of micronuclei may not be too reliable an indication of the monosomic condition.

Differences in sizes of univalents at metaphase I were established. No connection was found to exist between size of the monosome and the percentage of the quartets having micronuclei.

From a study of the distribution of the chromosomes at anaphase I and telophase I, it was concluded that there is a definite cycle for orientation and disjunction of bivalents and a definite cycle for univalents. The bivalent cycle precedes the univalent cycle and may exert an influence on the movement forces of the univalent.

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
LITERATURE REVIEW	3
Monosomics	3
Presence of Micronuclei	4
Behavior of Univalent Chromosomes	6
Interspecific Crosses	6
Intergeneric Crosses	9
Univalents in Monosomic Plants	10
Movement of Chromosomes	11
MATERIALS AND METHODS	12
Terminology	12
General Section	12
Examination for the Presence of Micronuclei in Quartets	13
Examination for the Presence of Micronuclei in Telo-interphase Cells	15
Metaphase I	16
Measurement of Metaphase I Univalents	16
Univalent Behavior at Anaphase I and Telophase I .	17
Chromosomes at Metaphase II and Anaphase II	17

TABLE OF CONTENTS (Continued)

	<u>Page</u>
RESULTS AND OBSERVATIONS	18
Preliminary Count	18
Second Count	20
Determination of a Critical Stage	22
Counts Within Monosomic Plants	27
Final Count of Quartets for the Twenty-one Monosomes	30
Additional Aberrations in Monosomic Lines	34
Normal Chinese Spring	35
Telo-interphase Counts	36
Metaphase I	41
Metaphase I Measurement of Univalent Chromosomes.	43
Chromosomes at Anaphase I and Telophase I	44
Metaphase II and Anaphase II Observations	49
DISCUSSION AND CONCLUSIONS	54
ACKNOWLEDGEMENTS	62
REFERENCES	63

[A](#)
 

[illegible][illegible]

THE BEHAVIOR OF THE UNIVALENT CHROMOSOMES OF
MONOSOMIC TRITICUM VULGARE AT MEIOSIS

J. W. Morrison

INTRODUCTION

During the first anaphase of normal meiosis bivalent chromosomes disjoin and migrate to opposite poles. If the chromosomal number includes a univalent chromosome there is no synapctic mate present to participate in this regular division and movement. It is recognized, therefore, that in plants which have univalent chromosomes the meiotic division will not proceed normally. This study was carried out to determine the behavior of the univalent chromosomes of monosomic Triticum vulgare at meiosis.

In particular the study was made to ascertain if differences or similarities of behavior existed among any of the twenty-one univalents of monosomic hexaploid wheat. It is apparent from the many published reports that there is still no

unanimity of opinion among cytologists regarding the behavior of the univalents at meiosis. It was felt that a study of single univalents would help to clarify the mechanism of their activity. It was thought too, that if there were major differences or similarities of behavior among certain chromosomes it would shed some light on the chromosome homologies and thus on the phylogeny of T. vulgare.

The two main problems studied were (a) the division of the univalent and (b) the formation of micronuclei in the microspores by the lagging univalent. The latter problem has become particularly important because the presence of micronuclei in the quartets of microspores has been used as an indication of the monosomic condition. Similarly the division or misdivision of the univalent, as well as the products of any such division, would have a direct bearing on the stability of the monosome and thus on the results of fundamental wheat breeding problems involving the use of monosomic plants.

In seeking an explanation for some of the results obtained, nearly all of the later phases of the meiotic cycle were examined. These observations are reported in this paper, together with information on the cytological technique employed in the examination of these phases of meiosis.

In so far as they have a bearing on the question of univalent behavior, this report also includes some cytological

1

 

observations on (a), a few additional aberrations other than monosomics and (b), normal wheat plants.

LITERATURE REVIEW

Monosomics

Monosomic plants are deficient for an entire chromosome. They have been obtained in several polyploid species. Unrau (24) gave a comprehensive review of the literature on monosomes and nullisomes. He also pointed out the advantages of their use for genetical studies in contrast to conventional methods.

The credit for obtaining, developing and numbering of the various monosomes, and for visualizing their great possibilities for genetical and breeding work of common wheat must go to Dr. E. R. Sears. He pioneered this field of research with his publications (17, 18).

Monosomic plants are now being used in breeding programs and genetical studies (12) at:

1. Dominion Laboratory of Cereal Breeding, Winnipeg, Manitoba.
2. Field Crop Insect Laboratory, Lethbridge, Alberta.
3. Central Experimental Farm, Ottawa, Ontario.
4. University of Alberta, Edmonton, Alberta.

Presence of Micronuclei

As indicated in the introduction, the presence of micronuclei in quartets has been used to identify monosomic plants. In 1932, Powers (10) examined the meiotic stages of monosomic plants and found that 23% of the quartets had micronuclei. The majority of the quartets having micronuclei contained only 1, but some with 2, 3 and 4 were also observed. He concluded that the presence of more than 1 micronucleus was probably caused by some other chromosomal aberration. He also reported the presence of micronuclei in 42.4% of the quartets from a plant with a chromosomal complement of $19'' 2'$. Differences in the percentage of quartets with micronuclei occurred within anthers; one count revealed that in the upper pollen sac 23.3% and in the lower sac only 1.6% of the quartets had micronuclei.

In the same year Powers (11) reported that in Marquis wheat 0.8% of the quartets had micronuclei, compared with 2.8%

in the variety Marquillo. A correlation was found to exist between the non-orientation and non-conjunction of chromosomes. The occurrence of micronuclei was an indication of the frequency of both types of these aberrations.

Myers and Powers (9), in 1938, found that in 41-chromosome wheat plants more than 20% of the quartets had micronuclei. They also concluded that heritable differences affected the number of micronuclei formed in normal plants. The percentages of quartets with micronuclei ranged from 0.8% in Thatcher to 8.3% in Supreme. Significant differences between the dates of collection of microspores indicated that environment may also be a factor in determining the difference in meiotic irregularities.

Love (8) found statistically significant differences in the frequencies of occurrence of micronuclei in quartets of 15 wheat hybrids. The percentages varied from 82 to 100 and the mean number of micronuclei per quartet ranged from 1.6 to 5.

In 1948, Howard (4) used the presence of micronuclei as an indication of abnormalities in the Picton variety of oats. He suspected variations in the percentage of quartets with micronuclei from late and early selected anthers. He found, however, from an examination of four slides for a number of plants studied, that there were no significant differences.

An investigation of the speltoid wheat of the B-series was conducted by Sanchez-Monge and MacKey (14), in 1948. They

used the classification of Huskins for speltoids and as such the chromosome complement of the B-series consisted of 40 chromosomes and 1 univalent or 40 chromosomes and 1 telocentric chromosome. In some of the quartets 0-4 micronuclei were noted. When there were 3 micronuclei in the quartet, one was always smaller than the other two; when there were 4, two of the micronuclei were smaller. While they did not report an actual percentage, the calculation from Table 4, page 328, shows that 73% of the quartets contained micronuclei. They attributed the formation of micronuclei to the lagging univalent.

Behavior of Univalent Chromosomes

The behavior of univalent or unpaired chromosomes has been reported by many authors (22, 15, 1, 7, 8, 25, 3, 16, 26, 6, 5, 21, 13). Most of these dealt with the behavior of the univalents formed from interspecific or intergeneric crosses.

Interspecific Crosses

In a cross of Triticum monococcum x Triticum turgidum, Thompson (22) observed that after the bivalents had divided, all

the univalents arranged themselves at the equator in regular fashion and each then divided equationally. Only rarely did one remain near the pole without dividing. At metaphase II the univalents remained near the centre undivided and then moved slowly at random to one pole or the other. Because of tardiness, several univalents failed to become incorporated in the new nucleus and formed small micronuclei.

Sax (15), who studied the same cross, reported a directly contrasting behavior of the univalents. At anaphase I, the univalents passed undivided at random to the poles. At anaphase II, the division of the bivalents and univalents was normal and seldom were any lagging chromosomes found. Few quartets with micronuclei were found.

According to Aase (1) most of the univalents of a triploid divided at anaphase I. The number that actually separated depended upon their location on the spindle at the time the equatorial split began.

Kihara (7) concluded that some univalents divide at first and lag at second division; others do not divide during first division but migrate at random to either pole. Those that divide at first division wandered at random to either pole in the second; the undivided univalents presumably divided normally.

There is more agreement among cytologists regarding the behavior of pentaploid univalents. Sax (15), Thompson (22),

Kihara (7), and Love (8), found that most of the univalents orientated on the equatorial plate after the bivalents divided. The univalents then split and passed poleward. At anaphase II, the lagging chromosomes did not divide but passed, apparently at random, to either pole. Micronuclei were observed in a few of the quartets. Aase (1) reported that none to all of the univalents divided equationally and although quartet formation was regular, one or sometimes two small micronuclei were formed.

Cytological studies of interspecific crosses in the genus Rubus L., were made by Vaarama (25). At metaphase I, univalents were scattered throughout the spindle. Some of them, apparently those which had lingered in the neighborhood of the poles, were included with the separated bivalents in the daughter nuclei. The remainder lagged near the plate, split and the halves moved poleward, but were usually not included in the interkinetic nuclei.

Gajewski (3) reported irregular behavior of univalents at meiosis in five interspecific Geum hybrids. In hybrids number 1 and 2, the 2-7 univalents mostly passed to the poles undivided at anaphase I. In hybrids 3 and 4, the 14 and 21 univalents respectively, lagged at the equator. Thereafter some divided, some passed poleward undivided and some remained passive in the cytoplasm. At interkinesis 12% of the cells showed the apparent loss of chromosomes into the cytoplasm. After the bivalents

divided in hybrid number 5, some of the univalents (42 univalents resulted from this cross) appeared to remain at the poles, others scattered on the spindle and the remaining few orientated at the plate. Those on the spindle moved unchanged to the poles; those at the plate divided. Gajewski suggested two main factors influencing the univalent action. First, the difference in genotypic constitution and secondly, the difference in numerical relationship between univalents and bivalents.

Intergeneric Crosses

In a cross of Aegilops cylindrica x Marquis (a common hexaploid wheat variety), Sax and Sax (16), reported that at anaphase I, the univalents were most frequently grouped at the poles. There was some division of lagging univalents, however, but usually all were included in the daughter nuclei at telophase I. In the second division some laggards were observed. They suggested that if the univalents did not divide in the first division they would divide in the second.

Wakar (26) concluded that univalents resulting from a Triticum x Agropyron cross may go undivided to either pole at random. There was marked lagging of chromosomes at the second division. The tardy chromosomes were transformed into lumps of chromatin (micronuclei).

Unpaired chromosomes arising from the cross of Triticum compactum x Secale cereale sometimes split and moved to opposite poles or the two split halves moved to the same pole according to Kagawa and Chizaki (6). In the second division, a great deal of irregularity of movement and lagging of chromosomes was observed and micronuclei frequently formed.

Univalents in Monosomic Plants

Huskins (5), from an examination of a 41-chromosome fatuoid oat plant, reported that in all of the 33 cells examined an univalent was lagging at the plate and splitting longitudinally at anaphase I. At telophase I, the halves of the univalent usually reached the poles before the nuclear membranes were formed. In a few of the cells, however, the daughter univalents were left out. In the second division there was usually one daughter univalent lagging at the plate in each of the daughter cells. Occasionally both were in one cell. The formation of quartets was not greatly affected although in a number, small dark bodies lying outside the nuclei were formed. These were likely split univalents which had failed to reach the poles before nuclear membranes were formed.

Smith et al (21) studied the behavior of chromosomes in a speltoid wheat plant with 20" 1'. As the bivalents passed

toward the poles at early anaphase I, the univalent moved to the plate. Then the univalent "split" longitudinally and its halves proceeded to opposite poles but very frequently arrived too late to be included in the daughter nuclei. The occurrence of "unsplit" univalents or the inclusion of the two halves in one dyad nucleus was not observed although genetical evidence indicated that it did occur. While transverse fragmentation was not observed in this strain, there was genetical evidence that it must have occurred. During the second division the daughter univalents were either left out of the microspore nuclei or were included without further splitting. From 150 pollen quartets it was calculated that 86% of the pollen grains contained only 20 chromosomes.

Movement of Chromosomes

A more accurate knowledge of the complicated phenomena of chromosome movement would no doubt throw some light on the question of univalent behavior. Sanchez-Monge (13), suggested that the movement of the univalent, at anaphase I, towards the equator was independent of centromeric forces. He concluded that normal disjunction was the result of normal insertion of the spindle fibres and erroneous insertion led to the misdivision of the univalent.

MATERIALS AND METHODS

Terminology

In concurrence with modern usage the following terminology was used:

1. first and second division instead of the older terms, heterotypic and homotypic division,
2. quartet for the group of four microspores arising from a spore mother cell, in preference to tetrad,
3. Mono-' ' to designate a plant deficient for a particular chromosome e.g. Mono-VI to denote a plant deficient for chromosome VI.

General Section

The 21 deficient lines of common wheat were obtained from the variety Chinese Spring, T. vulgare. Selfed monosomic plants give rise to nullisomics, normal and monosomics. Cytological examination of metaphase I of pollen mother cell meiosis was made in the selection of monosomic plants.

REPORT ON THE PROGRESS OF THE WORK

During the year 1900, the following work has been done:

1. GENERAL PRINCIPLES

The following principles have been adopted:

The first principle is that the work should be done in a systematic and methodical manner.

The second principle is that the work should be done in a thorough and complete manner.

The third principle is that the work should be done in a careful and accurate manner.

The fourth principle is that the work should be done in a prompt and efficient manner.

The fifth principle is that the work should be done in a consistent and uniform manner.

The sixth principle is that the work should be done in a clear and concise manner.

The seventh principle is that the work should be done in a logical and orderly manner.

The eighth principle is that the work should be done in a practical and useful manner.

The ninth principle is that the work should be done in a timely and expeditious manner.

2. SPECIFIC RESULTS

The following results have been obtained:

The first result is that the work has been done in a systematic and methodical manner.

The second result is that the work has been done in a thorough and complete manner.

The third result is that the work has been done in a careful and accurate manner.

The fourth result is that the work has been done in a prompt and efficient manner.

The fifth result is that the work has been done in a consistent and uniform manner.

The material used in the preliminary study was collected in 1949 and stored until used in May and June, 1950. In April, 1950, seed from each of the 21 different lines was planted in the field at two different dates. Heads were collected for cytological study in June. All material was killed and fixed in Carnoy's fluid A. All cytological observations were made from acetocarmine smear preparations as outlined by Smith (20). Some slight modifications employed are outlined in related following sections.

Photomicrographs were taken from freshly prepared slides at magnifications ranging from 360 to 800 diameters.

Examination for the Presence of Micronuclei in Quartets

The preliminary count was made under the following conditions. Approximately 1000 quartets from each monosome were examined. The counts were made on any anthers that were found to be in the quartet stage and no distinction was attempted between different plants representing a monosome or between anthers, florets or spikelets of a plant. This examination was made at a magnification of 120 diameters. Quartets were designated as (a) with micronuclei and (b) without micronuclei. The use of a

THE HISTORY OF THE CITY OF BOSTON

From the first settlement of the city in 1630 to the present time, the city has grown from a small fishing village to one of the largest and most important cities in the world. The city has been the center of many important events in American history, and it has played a major role in the development of the United States. The city has a rich and diverse culture, and it is a place where people from all over the world come to live and work. The city is a place of great beauty and interest, and it is a place that is worth visiting.

THE HISTORY OF THE CITY OF BOSTON

The city of Boston has a long and rich history, and it is a place that is full of life and energy. The city has been the center of many important events in American history, and it has played a major role in the development of the United States. The city has a rich and diverse culture, and it is a place where people from all over the world come to live and work. The city is a place of great beauty and interest, and it is a place that is worth visiting.

partially blackened-out eyepiece to limit the size of the field was employed for a time but its use was found unsatisfactory.

A second count was undertaken using a different procedure. All three anthers from a floret of a monosomic plant were smeared on a slide. An attempt was made to study at least 500 quartets per slide. Quartets were again classified into two categories but in those with micronuclei the number per quartet was noted.

A critical stage of quartet development was selected from information gained during the preliminary count and from the subsequent second count. At the stage selected, the majority of the quartets showed the formation of the cell wall at telophase II, prior to splitting apart or rounding up of microspores. A clear wall surrounded each quartet at this stage. This stage could be recognized during the preliminary inspection of the anther smear and only those that were at this stage were examined in detail. (Figs. 1 - 6, Plate 1, show quartets at the critical stage).

In the preparation of a slide for counting only slight pressure on the cover slip could be exerted to prevent rupturing of the quartets. It was therefore necessary to focus at various levels because all parts of the cell were not in the same optical plane.

... ..
... ..
... ..

... ..
... ..
... ..
... ..

... ..

... ..
... ..
... ..

... ..
... ..

... ..
... ..

... ..
... ..

... ..
... ..

... ..
... ..

... ..

Examination for the Presence of Micronuclei in
Telo-interphase Cells

Because wall formation at telophase I between the two daughter nuclei of a microsporocyte is not always definite and because cells at interphase in many instances had diffused nuclei, the counts were made at a stage approximately midway between the two (at telo-interphase). The time lapse of division from anaphase I to metaphase II is very short. It was frequently observed that all the cells from the three anthers were not at the same phase of division. A definite stage for examination was decided upon to insure accurate and comparable counts between different plants. At this stage both pre- and post-telo-interphase cells were present in approximately equal proportions with the majority of the cells at the desired stage. The telo-interphase cells were classified similarly to the quartets, i.e. (a) without and (b) with one micronucleus, etc.

Although at this stage of division greater pressure on the cover slip could be applied than at the quartet stage, excessive pressure ruptured the cells and made counting impossible. A magnification of 240 diameters was found satisfactory.

 

Metaphase I

Metaphase I was studied in determining which plants were monosomic. When the count of micronuclei in quartets was obviously irregular, the chromosome constitution was examined more closely. A magnification of 540 diameters was used for most observations but some of the critical examinations were made using the oil immersion objective at a magnification of 1080 diameters.

Measurement of Metaphase I Univalents

An attempt was made to determine the sizes of the various univalent chromosomes at metaphase I. The measurements were made with an eyepiece micrometer. For each monosome 30 determinations were made at a magnification of 540 diameters.

DECLARATION

I, the undersigned, do hereby declare that the information furnished by me in the foregoing questionnaire is true and correct to the best of my knowledge and belief, and that I am not aware of any facts or circumstances which would render the same misleading or incomplete.

Signature of Declarant

and I do hereby declare that I am not aware of any facts or circumstances which would render the foregoing information misleading or incomplete.

Univalent Behavior at Anaphase I and Telophase I

Anaphase I was studied to determine the distribution of bivalents and univalents at this phase. Where it was possible, counts were made of the dyads and monads. The division of the univalent was studied in detail.

Chromosomes at Metaphase II and Anaphase II

While a thorough study of the chromosomes at this stage of division was not attempted, some observations were recorded. The position, possible fragmentation and distribution of the chromosomes was examined in some detail but no count frequencies were established.

... ..

... ..

-
-
-

... ..

-
-
-
-

RESULTS AND OBSERVATIONS

Preliminary Count

The results of the preliminary count are given in Table 1. While there were variations from plant to plant in some monosomic lines, for others a set pattern seemed to be operative. There were indications that part of the variability was likely caused by examination of the quartets at different stages of development. Furthermore, all preliminary experiments led to the conclusion that a greater magnification was necessary for these examinations.

Table 1

Micronuclei Observed in Quartets - Preliminary Count

Monosome studied*	No. of plants	No. of Qs.** counted	Qs. with Mn.** in %
I	4	1392	35.3
II	2	1481	50.8
III	4	1217	55.4
IV	3	1132	56.5
V	2	1030	55.3
VI	4	1097	56.8
VII	6	1474	50.0
VIII	5	1159	35.4
IX	3	1101	65.0
X	3	1211	49.7
XI	3	1426	60.0
XII	2	1004	47.2
XIII	7	1694	66.0
XVI	2	613	64.6
XVII	5	1236	49.9
XVIII	4	1306	57.4
XIX	3	1043	51.4
XX	3	1105	60.6
XXI	5	1586	47.2

* Monosomes XIV and XV were not available for this study.

** Qs. Hereafter tabular abbreviation for quartet.
Mn. Hereafter tabular abbreviation for micronuclei.

THE JOURNAL OF THE AMERICAN MEDICAL ASSOCIATION PUBLISHED WEEKLY

Subscription prices: Five dollars per annum in advance. Single copies, fifteen cents. Payment in advance. All communications should be addressed to the Editor, The Journal of the American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Entered as second-class matter, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Acceptance for mailing at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917.

Published by The American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Copyright, 1918, by The American Medical Association

Printed at the Chicago Press, Chicago, Ill.

Subscription prices: Five dollars per annum in advance. Single copies, fifteen cents. Payment in advance. All communications should be addressed to the Editor, The Journal of the American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Entered as second-class matter, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Acceptance for mailing at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917.

Published by The American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Copyright, 1918, by The American Medical Association

Printed at the Chicago Press, Chicago, Ill.

Subscription prices: Five dollars per annum in advance. Single copies, fifteen cents. Payment in advance. All communications should be addressed to the Editor, The Journal of the American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Entered as second-class matter, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Acceptance for mailing at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917.

Published by The American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Copyright, 1918, by The American Medical Association

Printed at the Chicago Press, Chicago, Ill.

Subscription prices: Five dollars per annum in advance. Single copies, fifteen cents. Payment in advance. All communications should be addressed to the Editor, The Journal of the American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Entered as second-class matter, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Acceptance for mailing at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917.

Published by The American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Copyright, 1918, by The American Medical Association

Printed at the Chicago Press, Chicago, Ill.

Subscription prices: Five dollars per annum in advance. Single copies, fifteen cents. Payment in advance. All communications should be addressed to the Editor, The Journal of the American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Entered as second-class matter, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Acceptance for mailing at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917.

Published by The American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Copyright, 1918, by The American Medical Association

Printed at the Chicago Press, Chicago, Ill.

Subscription prices: Five dollars per annum in advance. Single copies, fifteen cents. Payment in advance. All communications should be addressed to the Editor, The Journal of the American Medical Association, 535 North Dearborn Street, Chicago, Ill.

Entered as second-class matter, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Acceptance for mailing at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917. Postpaid at special rate of \$4.00 per annum authorized by Act of Congress, October 3, 1917.

Second Count

The difference between monosomes observed during the preliminary count suggested a definite behavior of univalents in the formation of micronuclei. It was felt that a more careful count at higher magnification and statistical analysis of results would confirm or disprove this hypothesis.

In Table 2, the results of the second count are recorded. Statistical analysis indicated that there were significant differences between some of the monosomes. In the comparison of the mean percentages of quartets with micronuclei of the various monosomes, with the results obtained in the preliminary count, 9 out of 19 monosomes agreed within 3%. The difference ranged from 1.1 to 18.5%. From the regularity of some lines and the irregularity of others, it was apparent that either the formation of micronuclei was uniform for some monosomes and not for others, or that these differences were caused by errors suggested from observations made during the preliminary count.

The three major possibilities for error indicated from the preliminary observation were:

1. breaking up of quartets into dispersed microspores,
2. loss of micronuclei by isolation of microcytes (miniature microspores),
3. disappearance of micronuclei by absorption into the cytoplasm or the nucleus.

Table 2

Micronuclei Observed in Quartets - Second Count

Monosome studied	Plant 1		Plant 2		Mean
	No. of Qs. counted	Qs. with Mn. in %	No. of Qs. counted	Qs. with Mn. in %	Qs. with Mn. in %
I	585	35.2	539	33.1	34.2
II	824	70.3	620	68.2	69.3
III	597	58.5	722	47.1	52.8
IV	669	59.5	637	59.2	59.4
V	574	59.8	829	56.2	58.0
VI	528	42.4	623	50.1	46.3
VII	818	50.2	485	34.9	42.6
VIII	679	34.2	528	33.7	34.0
IX	508	52.8	566	45.6	49.2
X	726	36.0	560	36.3	36.2
XI	662	53.3	621	50.7	52.0
XII	516	31.2	613	36.4	33.8
XIII	540	65.2	500	59.4	62.3
XIV	837	58.3	540	55.6	57.0
XV	743	48.1	624	41.2	44.7
XVI	601	55.9	789	47.8	51.9
XVII	516	46.3	672	47.9	47.1
XVIII	804	50.0	645	49.2	49.6
XIX	747	37.9	513	32.4	35.2
XX	720	58.6	563	60.0	59.3
XXI	786	48.7	571	41.9	45.3

M.S.D. = 8.5%.

Table 1

Table 1. Summary of the results of the analysis of variance for the effect of the treatment on the response of the different groups of subjects.

Group	Treatment	Response	Significance	Mean	Standard Error
1	Control	1.0	0.05	1.0	0.1
2	Control	1.0	0.05	1.0	0.1
3	Control	1.0	0.05	1.0	0.1
4	Control	1.0	0.05	1.0	0.1
5	Control	1.0	0.05	1.0	0.1
6	Control	1.0	0.05	1.0	0.1
7	Control	1.0	0.05	1.0	0.1
8	Control	1.0	0.05	1.0	0.1
9	Control	1.0	0.05	1.0	0.1
10	Control	1.0	0.05	1.0	0.1
11	Control	1.0	0.05	1.0	0.1
12	Control	1.0	0.05	1.0	0.1
13	Control	1.0	0.05	1.0	0.1
14	Control	1.0	0.05	1.0	0.1
15	Control	1.0	0.05	1.0	0.1
16	Control	1.0	0.05	1.0	0.1
17	Control	1.0	0.05	1.0	0.1
18	Control	1.0	0.05	1.0	0.1
19	Control	1.0	0.05	1.0	0.1
20	Control	1.0	0.05	1.0	0.1
21	Control	1.0	0.05	1.0	0.1
22	Control	1.0	0.05	1.0	0.1
23	Control	1.0	0.05	1.0	0.1
24	Control	1.0	0.05	1.0	0.1
25	Control	1.0	0.05	1.0	0.1
26	Control	1.0	0.05	1.0	0.1
27	Control	1.0	0.05	1.0	0.1
28	Control	1.0	0.05	1.0	0.1
29	Control	1.0	0.05	1.0	0.1
30	Control	1.0	0.05	1.0	0.1
31	Control	1.0	0.05	1.0	0.1
32	Control	1.0	0.05	1.0	0.1
33	Control	1.0	0.05	1.0	0.1
34	Control	1.0	0.05	1.0	0.1
35	Control	1.0	0.05	1.0	0.1
36	Control	1.0	0.05	1.0	0.1
37	Control	1.0	0.05	1.0	0.1
38	Control	1.0	0.05	1.0	0.1
39	Control	1.0	0.05	1.0	0.1
40	Control	1.0	0.05	1.0	0.1
41	Control	1.0	0.05	1.0	0.1
42	Control	1.0	0.05	1.0	0.1
43	Control	1.0	0.05	1.0	0.1
44	Control	1.0	0.05	1.0	0.1
45	Control	1.0	0.05	1.0	0.1
46	Control	1.0	0.05	1.0	0.1
47	Control	1.0	0.05	1.0	0.1
48	Control	1.0	0.05	1.0	0.1
49	Control	1.0	0.05	1.0	0.1
50	Control	1.0	0.05	1.0	0.1
51	Control	1.0	0.05	1.0	0.1
52	Control	1.0	0.05	1.0	0.1
53	Control	1.0	0.05	1.0	0.1
54	Control	1.0	0.05	1.0	0.1
55	Control	1.0	0.05	1.0	0.1
56	Control	1.0	0.05	1.0	0.1
57	Control	1.0	0.05	1.0	0.1
58	Control	1.0	0.05	1.0	0.1
59	Control	1.0	0.05	1.0	0.1
60	Control	1.0	0.05	1.0	0.1
61	Control	1.0	0.05	1.0	0.1
62	Control	1.0	0.05	1.0	0.1
63	Control	1.0	0.05	1.0	0.1
64	Control	1.0	0.05	1.0	0.1
65	Control	1.0	0.05	1.0	0.1
66	Control	1.0	0.05	1.0	0.1
67	Control	1.0	0.05	1.0	0.1
68	Control	1.0	0.05	1.0	0.1
69	Control	1.0	0.05	1.0	0.1
70	Control	1.0	0.05	1.0	0.1
71	Control	1.0	0.05	1.0	0.1
72	Control	1.0	0.05	1.0	0.1
73	Control	1.0	0.05	1.0	0.1
74	Control	1.0	0.05	1.0	0.1
75	Control	1.0	0.05	1.0	0.1
76	Control	1.0	0.05	1.0	0.1
77	Control	1.0	0.05	1.0	0.1
78	Control	1.0	0.05	1.0	0.1
79	Control	1.0	0.05	1.0	0.1
80	Control	1.0	0.05	1.0	0.1
81	Control	1.0	0.05	1.0	0.1
82	Control	1.0	0.05	1.0	0.1
83	Control	1.0	0.05	1.0	0.1
84	Control	1.0	0.05	1.0	0.1
85	Control	1.0	0.05	1.0	0.1
86	Control	1.0	0.05	1.0	0.1
87	Control	1.0	0.05	1.0	0.1
88	Control	1.0	0.05	1.0	0.1
89	Control	1.0	0.05	1.0	0.1
90	Control	1.0	0.05	1.0	0.1
91	Control	1.0	0.05	1.0	0.1
92	Control	1.0	0.05	1.0	0.1
93	Control	1.0	0.05	1.0	0.1
94	Control	1.0	0.05	1.0	0.1
95	Control	1.0	0.05	1.0	0.1
96	Control	1.0	0.05	1.0	0.1
97	Control	1.0	0.05	1.0	0.1
98	Control	1.0	0.05	1.0	0.1
99	Control	1.0	0.05	1.0	0.1
100	Control	1.0	0.05	1.0	0.1

It was realized during the second count that breaking up of the quartets was responsible for some of the variability within plants of a certain monosome.

Determination of the Critical Stage

It was decided to make further counts of quartets from individual plants to see if there were variations within one spike and to see if any evidence could be found to substantiate the suggested possibilities for error. In any event a critical stage had to be established to keep future counts comparable.

For this study, plant 98A-2, Mono-III, was selected. The results are summarized in Table 3. There was a tendency for the formation of microcytes at older stages of development of some of the quartets. Even with the slight pressure used to clear a slide of air bubbles, some microcytes were forced out of the quartet arrangement and would therefore be missed in counting. (Figs. 2, 3, 4 and 5, Plate 2, illustrate some of the conditions observed). When these counts were being made the stage for each count was designated as young when no breaking up had occurred and as old when a number of quartets had broken up. The difference between counts of old and young quartets was striking. Statistical analysis revealed that counts 1 and 4 were significantly below the other three. The lower percentage of quartets with micronuclei in counts 1 and 4 was undoubtedly brought about by a loss of microcytes in older quartets.

Table 3

Micronuclei Observed in Quartets - Effect of Stage of Quartet
Development

Monosome studied	Plant No.	Count No.	No. of Qs. counted	Qs. with Mn. in %	Stage of Qs. development
III	98A-2	1	517	32.9	Old
		2	588	48.6	Young
		3	554	56.5	Young
		4	389	37.0	Old
		5	619	50.9	Young
II	97A-21	1	641	66.3	Young, reliable
		2	555	47.8	Old, unreliable
		3	753	65.6	Young, reliable
		4	710	67.5	Young, reliable

Plate 1.

Quartets at the Critical Stage

- Fig. 1. Without micronuclei.
Fig. 2. With one micronucleus.
Fig. 3. With two micronuclei in one microspore.
Fig. 4. With two micronuclei, one in each daughter cell.
Fig. 5. With three micronuclei.
Fig. 6. With four micronuclei.

(Magnification 500 X)

Table 1

Summary of the results

1. The first group of results shows that the average value of the variable is 1.2.	1.2
2. The second group of results shows that the average value of the variable is 1.5.	1.5
3. The third group of results shows that the average value of the variable is 1.8.	1.8
4. The fourth group of results shows that the average value of the variable is 2.1.	2.1
5. The fifth group of results shows that the average value of the variable is 2.4.	2.4
6. The sixth group of results shows that the average value of the variable is 2.7.	2.7
7. The seventh group of results shows that the average value of the variable is 3.0.	3.0
8. The eighth group of results shows that the average value of the variable is 3.3.	3.3
9. The ninth group of results shows that the average value of the variable is 3.6.	3.6
10. The tenth group of results shows that the average value of the variable is 3.9.	3.9

Plate 2

Micronuclei in Quartets

- Fig. 1. With six micronuclei. (Quartet at critical stage).
Fig. 2. Advanced stage of development, isolated microcyte.
Fig. 3. Advanced stage of development, isolated micronuclei.
Fig. 4. Advanced stage of development, isolated microcyte.
Fig. 5. Advanced stage of development, microcyte lost from quartet arrangement.
Fig. 6. Faded micronucleus.

(Magnification 500 X)

TABLE I

Summary of Results

1.	First trial (100%)	100%
2.	Second trial (100%)	100%
3.	Third trial (100%)	100%
4.	Fourth trial (100%)	100%
5.	Fifth trial (100%)	100%
6.	Sixth trial (100%)	100%
7.	Seventh trial (100%)	100%
8.	Eighth trial (100%)	100%
9.	Ninth trial (100%)	100%
10.	Tenth trial (100%)	100%

As a further check on the correctness of this conclusion, a number of counts were made using plant 97A-21, Mono-II. Here the stages were designated as young or old (reliable or unreliable) before the count was made. The results in Table 3 show that counts were similar when the stage designated as young or reliable was examined. When an old stage was counted, the percentage of quartets with micronuclei was significantly lowered.

The possibility that micronuclei were absorbed at later stages of quartet development was not disregarded. An examination of dispersed microspores revealed the presence of micronuclei. This examination was extended to later developmental stages, where some of the microspores had formed the cellulose intine walls. The micronuclei, when present, were small dark bodies and indistinguishable from the micronuclei observed in quartet microspores. It appears probable that micronuclei can be lost from microspores prior to intine wall formation.

Results similar to those reported above have been obtained by other workers. Frankel (2) reported that microcytes were formed from lagging centric and acentric fragments of wheat chromosomes. Thompson and Hollingshead (23) found a slight decrease in number of micronuclei from the conclusion of second division to the separation of microspores. These two authors believed that micronuclei were reabsorbed by nuclei, or that they degenerate.

Counts Within Monosomic Plants

The hypothesis that the formation of micronuclei was uniform within one plant was further confirmed by the results given in Table 4. Most of these counts were made after the critical stage had been decided upon. The variability observed between counts of the same plant was non-significant.

These results agreed with the results obtained by Howard, but are seemingly contradictory to the conclusions of Powers (c.f. literature review). The regularity of the formation of micronuclei in different florets of the same plant suggested a regular formation in the individual anthers. A study of single anthers was made and the results are given in Table 5. No statistical analysis is necessary to show the similarities between the three anthers of the one floret.

These results, therefore, indicate that within any spike, micronuclei are formed with equal frequency in the various florets or anthers.

Table 4

Micronuclei Observed in Quartets - Counts Within Plants

Monosome studied	Plant No.	No. of Qs. counted	Qs. with Mn. in %
V	00-22	738	56.8
	"	636	56.9
X	05-4	560	36.3
	"	620	34.8
XI	06-5	621	50.7
	"	625	50.2
XIV	09-18	837	58.3
	"	597	57.1
	09-25	540	55.6
	"	607	51.1
XVI	11A-20	601	55.9
	"	670	57.6
XVIII	13-19	804	50.0
	"	892	50.9
XXI	16-16	631	46.9
	"	554	46.4

Table 5

Micronuclei Observed in Quartets - Anther Count

Monosome studied	Plant No.	Anther No.	No. of Qs. counted	Qs. with Mn. in %
XII	07-2	1	242	39.7
		2	245	41.2
		3	222	42.8
IV	99-5	1	186	66.7
		2	243	65.0
		3	214	65.9
XVIII	13-19	1	360	51.7
		2	318	48.7
		3	214	52.8
XX	15A-9	1	303	54.5
		2	367	54.2
		3	247	55.5

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Содержание

Final Count of Quartets for the Twenty-one Monosomes

After the establishment of a critical stage of quartet development and with the practice acquired from previous counting, it was decided to make final quartet counts of three different plants for each monosome. The percentages of quartets with micronuclei for each of the different lines are tabulated in Table 6. The monosomes are listed in order of increasing frequency of quartets with micronuclei.

Although approximately 20 heads were fixed and stored for each monosome, in some lines more normal plants than were expected on the basis of 75:25-distribution (Sears (18)) were present. This can partly be explained on the basis that some monosomic plants do not mature as early as normal plants. The random selection included more of these normal plants. Consequently, only two monosomic plants were available for monosomes, VIII, IX, XIII, XV and XVII, for this count. In order that the estimation of the means for this final count could be kept comparable, one of the counts obtained in the previous study was included for each of the five monosomes.

Table 6

Micronuclei Observed in Quartets - Final Count

Monosome studied	Plant 1		Plant 2		Plant 3		Mean Qs. with Mn. in %
	No. of counted	Qs. with Mn. in %	No. of counted	Qs. with Mn. in %	No. of counted	Qs. with Mn. in %	
X	620	34.8	700	32.4	626	35.0	34.1
VIII	679	34.2	469	35.2	503	33.6	34.3
I	369	39.0	621	40.9	604	37.1	39.0
XII	554	40.8	569	39.2	709	41.2	40.4
XV	624	41.2	575	40.2	601	40.4	40.6
XXI	631	46.9	625	45.6	563	42.3	44.9
VII	593	47.4	525	44.6	656	47.6	46.5
XI	625	50.2	618	44.7	636	47.2	47.4
IX	566	45.2	520	45.8	555	52.1	47.7
III	674	45.5	648	46.6	635	51.4	47.8
VI	694	50.9	540	49.4	558	48.9	49.7
XVII	672	47.9	405	52.1	618	50.3	50.1
XVIII	554	48.9	566	50.7	892	50.9	50.2
XIV	607	51.1	597	57.1	573	57.1	55.1
V	829	56.2	738	56.8	541	53.6	55.5
XVI	670	59.0	606	57.6	422	55.7	57.4
XIX	640	58.3	809	61.6	562	60.7	60.2
XIII	540	65.2	500	59.4	562	64.2	62.9
XX	608	66.8	618	57.9	720	65.3	63.3
IV	548	63.1	604	65.6	643	65.8	64.8
II	753	65.6	543	66.3	569	63.8	65.2

M.S.D. = 3.8%.

Mean = 50.3%.

With the exception of Mono-XIX, the differences in means obtained in the second and final count were within a range of 0.4 to 6.6%. In Mono-XIX, where the difference was 25%, it was possible to determine the cause of this difference. One of the plants used in the second count had been saved and two further examinations of quartets at the critical stage were made. The percentages of quartets with micronuclei were 58% and 63% respectively. Likely the second count in both plants was made from an unsuitable (too old) stage of the quartet development.

Analysis of variance showed a significant difference between chromosomes. Inspection of the plant results shows that very little variability existed between plants of the same monosome.

In Table 7 the distribution of quartets containing from 1 to over 4 micronuclei is shown. (Figs. 2, 3, 4, 5, 6, Plate 1 and Fig. 1, Plate 2, show quartets with different numbers of micronuclei). The significance and probable source of the higher numbers of micronuclei per quartet will be discussed in a later section.

Table 7

Number of Micronuclei per Quartet

Monosome studied	Frequency of Mn. per Qs. in %				
	1 Mn.	2 Mn.	3 Mn.	4 Mn.	Over 4 Mn.
X	59.7	33.2	6.8	0.3	-
VIII	56.5	33.0	8.5	1.1	0.9
I	68.3	27.2	3.5	1.0	-
XII	57.8	36.6	4.7	0.9	-
XV	61.0	33.8	3.2	1.9	0.1
XXI	57.6	36.5	5.4	0.4	0.1
VII	55.7	35.4	7.6	1.1	0.2
XI	54.5	39.1	5.4	1.0	-
IX	52.2	34.0	10.2	2.8	0.8
III	55.8	35.6	7.3	1.3	-
VI	65.1	31.1	3.5	0.3	-
XVII	63.2	28.8	6.3	1.3	0.4
XVIII	50.1	36.6	9.2	3.2	0.9
XIV	49.3	41.1	7.2	1.4	1.0
V	49.1	39.7	8.2	2.4	0.6
XVI	55.8	37.9	5.6	0.6	0.1
XIX	59.1	32.1	7.4	0.8	0.6
XIII	49.3	41.1	7.2	1.4	1.0
XX	44.0	46.8	7.3	1.6	0.3
IV	44.7	43.6	8.7	2.3	0.7
II	47.4	42.5	8.1	1.6	0.3
Range	68.3-44.0	46.8-27.2	10.2-3.2	3.2-.3	1.0-0.0
Mean	54.1	37.2	6.9	1.4	.4

Table 1

Summary of the data collected during the experiment

Experiment 1					Experiment 2				
Time	Temp	Humidity	Wind	Pressure	Time	Temp	Humidity	Wind	Pressure
10:00	25.0	60.0	1.0	1013.0	10:00	25.0	60.0	1.0	1013.0
10:15	25.5	61.0	1.1	1013.5	10:15	25.5	61.0	1.1	1013.5
10:30	26.0	62.0	1.2	1014.0	10:30	26.0	62.0	1.2	1014.0
10:45	26.5	63.0	1.3	1014.5	10:45	26.5	63.0	1.3	1014.5
11:00	27.0	64.0	1.4	1015.0	11:00	27.0	64.0	1.4	1015.0
11:15	27.5	65.0	1.5	1015.5	11:15	27.5	65.0	1.5	1015.5
11:30	28.0	66.0	1.6	1016.0	11:30	28.0	66.0	1.6	1016.0
11:45	28.5	67.0	1.7	1016.5	11:45	28.5	67.0	1.7	1016.5
12:00	29.0	68.0	1.8	1017.0	12:00	29.0	68.0	1.8	1017.0
12:15	29.5	69.0	1.9	1017.5	12:15	29.5	69.0	1.9	1017.5
12:30	30.0	70.0	2.0	1018.0	12:30	30.0	70.0	2.0	1018.0
12:45	30.5	71.0	2.1	1018.5	12:45	30.5	71.0	2.1	1018.5
13:00	31.0	72.0	2.2	1019.0	13:00	31.0	72.0	2.2	1019.0
13:15	31.5	73.0	2.3	1019.5	13:15	31.5	73.0	2.3	1019.5
13:30	32.0	74.0	2.4	1020.0	13:30	32.0	74.0	2.4	1020.0
13:45	32.5	75.0	2.5	1020.5	13:45	32.5	75.0	2.5	1020.5
14:00	33.0	76.0	2.6	1021.0	14:00	33.0	76.0	2.6	1021.0
14:15	33.5	77.0	2.7	1021.5	14:15	33.5	77.0	2.7	1021.5
14:30	34.0	78.0	2.8	1022.0	14:30	34.0	78.0	2.8	1022.0
14:45	34.5	79.0	2.9	1022.5	14:45	34.5	79.0	2.9	1022.5
15:00	35.0	80.0	3.0	1023.0	15:00	35.0	80.0	3.0	1023.0
15:15	35.5	81.0	3.1	1023.5	15:15	35.5	81.0	3.1	1023.5
15:30	36.0	82.0	3.2	1024.0	15:30	36.0	82.0	3.2	1024.0
15:45	36.5	83.0	3.3	1024.5	15:45	36.5	83.0	3.3	1024.5
16:00	37.0	84.0	3.4	1025.0	16:00	37.0	84.0	3.4	1025.0
16:15	37.5	85.0	3.5	1025.5	16:15	37.5	85.0	3.5	1025.5
16:30	38.0	86.0	3.6	1026.0	16:30	38.0	86.0	3.6	1026.0
16:45	38.5	87.0	3.7	1026.5	16:45	38.5	87.0	3.7	1026.5
17:00	39.0	88.0	3.8	1027.0	17:00	39.0	88.0	3.8	1027.0
17:15	39.5	89.0	3.9	1027.5	17:15	39.5	89.0	3.9	1027.5
17:30	40.0	90.0	4.0	1028.0	17:30	40.0	90.0	4.0	1028.0
17:45	40.5	91.0	4.1	1028.5	17:45	40.5	91.0	4.1	1028.5
18:00	41.0	92.0	4.2	1029.0	18:00	41.0	92.0	4.2	1029.0
18:15	41.5	93.0	4.3	1029.5	18:15	41.5	93.0	4.3	1029.5
18:30	42.0	94.0	4.4	1030.0	18:30	42.0	94.0	4.4	1030.0
18:45	42.5	95.0	4.5	1030.5	18:45	42.5	95.0	4.5	1030.5
19:00	43.0	96.0	4.6	1031.0	19:00	43.0	96.0	4.6	1031.0
19:15	43.5	97.0	4.7	1031.5	19:15	43.5	97.0	4.7	1031.5
19:30	44.0	98.0	4.8	1032.0	19:30	44.0	98.0	4.8	1032.0
19:45	44.5	99.0	4.9	1032.5	19:45	44.5	99.0	4.9	1032.5
20:00	45.0	100.0	5.0	1033.0	20:00	45.0	100.0	5.0	1033.0

Additional Aberrations in Monosomic Lines

The presence of micronuclei was frequently used as an indication that a plant was monosomic, when selecting anthers for quartet examination. In all cases, however, metaphase I was studied to verify this supposition. Frequently this latter study was made after the quartet count had been established. This procedure was followed with plant 15-H in which 79.8% of the quartets had micronuclei. The metaphase examination revealed the constitution of this plant to be 19" 2' and not 20" 1', as was expected (Fig. 4, Plate 4). In three other plants, aberrations other than the monosomic condition were found. (Fig. 5, Plate 4, shows the chromosomal complement of plant 09-A.) The percentages of quartets with micronuclei were established for four of these plants and are recorded in Table 8.

Of the four plants studied, the presence of extra univalents or fragments caused a marked increase in the number of quartets with micronuclei. The presence of a fragment increased the percentage by approximately 20. The number of micronuclei varied from 0 to 9. In plant 09-A, one further count was made to determine if this aberrant condition affected the formation of micronuclei uniformly throughout the spike. The results obtained indicate a regular formation within this plant.

Table 8

Micronuclei Observed in Quartets - Comparison of Aberrant
with Related Monosomic Plants

Monosomic line	Plant No.	Metaphase configuration	No. of Qs. counted	Qs. with Mn. in %	Related mono.
					Qs. with Mn. in %
XX	15-H	19" 2'	367	79.8	63.3
XIV	09-A	20" 1' 1 f.	578	71.8	55.1
IX	04-C	19" 1' 1 f.	378	72.7	47.7
X	05A-9	18" 5' or 18" 1" 2'	653	47.0	34.1
	05A-9	18" 5' or 18" 1" 2'	671	45.3	34.1

Normal Chinese Spring

Counts of quartets were made from normal Chinese Spring plants to ascertain if micronuclei were present and if so, in what proportions. These results are presented in Table 9. There were no statistical differences between the counts involving five different plants. The number of micronuclei per quartet varied from 0 to 4 and of the quartets having micronuclei, 55.6% had 1, 31.2% had 2, 9% had 3 and 4.2% had 4 micronuclei.

ANNUAL REPORT OF THE COMMISSIONER OF THE LAND OFFICE FOR THE YEAR 1900

Year	Area	Value	Per cent	Per cent	Per cent
1900	1,200	100	100	100	100
1901	1,200	100	100	100	100
1902	1,200	100	100	100	100
1903	1,200	100	100	100	100
1904	1,200	100	100	100	100
1905	1,200	100	100	100	100
1906	1,200	100	100	100	100
1907	1,200	100	100	100	100
1908	1,200	100	100	100	100
1909	1,200	100	100	100	100
1910	1,200	100	100	100	100

ANNUAL REPORT OF THE COMMISSIONER OF THE LAND OFFICE FOR THE YEAR 1900

The following table shows the results of the work of the Land Office during the year 1900. The table is divided into two parts, the first showing the results of the work of the Land Office during the year 1900, and the second showing the results of the work of the Land Office during the year 1901.

The first part of the table shows the results of the work of the Land Office during the year 1900. The table is divided into two columns, the first showing the results of the work of the Land Office during the year 1900, and the second showing the results of the work of the Land Office during the year 1901.

The second part of the table shows the results of the work of the Land Office during the year 1901. The table is divided into two columns, the first showing the results of the work of the Land Office during the year 1901, and the second showing the results of the work of the Land Office during the year 1902.

Table 9

Micronuclei Observed in Quartets - Normal Chinese Spring

Plant No.	No. of Qs. counted	Qs. with Mn. in %
1	520	3.5
2	526	4.6
3	672	6.0
4	510	6.1
5	628	4.5

Mean = 5.0%.

Telo-interphase Counts

During the examination of anther smears, it was noted that micronuclei were also present at the telo-interphase stage of cell division. In a count of 1044 cells from three normal Chinese Spring plants, 53 or 5.1% had micronuclei. As this frequency was similar to the percentage of quartets with micronuclei (5.0%), counts were made to determine if in monosomic plants a correlation existed between the number of quartets with micronuclei and the number of telo-interphase cells with micronuclei. Twenty-six plants from six different monosomes were studied and the results are summarized in Table 10.

Table 10

Micronuclei Observed in Telo-interphase Cells - Comparison
of Quartets with Micronuclei in Related Monosomes

Monosome studied	No. of cells counted	Cells with Mn. in %	Mean in %	Qs. with Mn. in % (final count)
XII	274	42.3	43.8	40.4
	246	46.3		
	316	49.1		
	334	40.1		
	338	44.4		
	196	43.4		
	198	40.4		
VIII	269	33.5	32.2	34.3
	150	31.3		
	215	31.6		
	276	31.2		
IV	368	42.4	41.6	64.8
	336	41.1		
	411	41.4		
	280	41.4		
XXI	281	45.2	44.2	44.9
	355	45.9		
	311	43.1		
	300	42.3		
XVIII	359	45.4	46.2	50.2
	203	47.8		
	407	46.9		
	268	44.2		
II	267	62.6	58.7	65.2
	126	59.5		
	335	55.2		

THE UNIVERSITY OF CHICAGO
 	
		100	

With the exception of the count from plant 4 in Mono-XII, the differences between plants of any monosome were not significant. The count of plant 4 was just significantly lower than plant 3. Since this was the only exception, it was concluded that this exception was not too important.

The correlation between the percentage of telo-interphase cells with micronuclei and the final computed percentage of the quartets with micronuclei was not significant ($r = +.687$). Examination of the results in Table 10 reveals that this low correlation value was greatly affected by the results of Mono-XII and Mono-IV. The correlation of the four remaining monosomes was highly significant ($r = +.992$).

Analysis of variance indicated that there were significant differences between some of the monosomes in the number of micronuclei observed at telo-interphase.

The distribution of the telo-interphase cells having micronuclei is given in Table 11. (Figs. 1 - 6, Plate 3, show cells with different numbers of micronuclei). Three and 4 micronuclei per cell were observed but in only one cell out of over 3,000 were more than 4 micronuclei found. It is striking, that in telo-interphase the proportions of cells with 1 and 2 micronuclei are not very dissimilar in different monosomes. It will be recalled that in the quartet study, there were very marked differences between the various monosomes.

Table 11

Number of Micronuclei per Telo-interphase Cell

Monosome studied	Frequency of Mn. per cell in %				
	1 Mn.	2 Mn.	3 Mn.	4 Mn.	Over 4 Mn.
VIII	77.3	19.9	2.1	.7	-
XII	69.4	29.1	.8	.7	-
IV	81.4	17.3	1.0	.3	-
XXI	72.1	25.0	2.4	.5	-
XVIII	69.7	28.2	1.8	.3	-
II	72.4	25.1	1.9	.5	.2
Mean	73.1	24.8	1.5	.5	0.0

TABLE I

Summary of the results of the experiments on the effect of the concentration of the solution on the rate of the reaction

Concentration of the solution (M)					Rate of the reaction (M/min)
0.1	0.2	0.3	0.4	0.5	0.15
0.2	0.3	0.4	0.5	0.6	0.25
0.3	0.4	0.5	0.6	0.7	0.35
0.4	0.5	0.6	0.7	0.8	0.45
0.5	0.6	0.7	0.8	0.9	0.55
0.6	0.7	0.8	0.9	1.0	0.65
0.7	0.8	0.9	1.0	1.1	0.75
0.8	0.9	1.0	1.1	1.2	0.85
0.9	1.0	1.1	1.2	1.3	0.95
1.0	1.1	1.2	1.3	1.4	1.05

Plate 3

Micronuclei at Telo-interphase

Fig. 1. One cell without micronuclei, one with one micronucleus.

Fig. 2. With one micronucleus.

Fig. 3. With two micronuclei.

Fig. 4. With two micronuclei near one daughter nucleus.

Fig. 5. With three micronuclei.

Fig. 6. With four micronuclei.

(Magnification 500 X)

TABLE

Summary of the results of the investigation

1. The results of the investigation are as follows:	1.1. The results of the investigation are as follows:	1.2. The results of the investigation are as follows:
2. The results of the investigation are as follows:	2.1. The results of the investigation are as follows:	2.2. The results of the investigation are as follows:
3. The results of the investigation are as follows:	3.1. The results of the investigation are as follows:	3.2. The results of the investigation are as follows:
4. The results of the investigation are as follows:	4.1. The results of the investigation are as follows:	4.2. The results of the investigation are as follows:
5. The results of the investigation are as follows:	5.1. The results of the investigation are as follows:	5.2. The results of the investigation are as follows:
6. The results of the investigation are as follows:	6.1. The results of the investigation are as follows:	6.2. The results of the investigation are as follows:
7. The results of the investigation are as follows:	7.1. The results of the investigation are as follows:	7.2. The results of the investigation are as follows:
8. The results of the investigation are as follows:	8.1. The results of the investigation are as follows:	8.2. The results of the investigation are as follows:

Metaphase I ---

In the majority of cells at metaphase I, the univalents were lying off the metaphase plate. This is in agreement with the observations of other workers (c.f. literature review).

Metaphase I of 16 plants representing four different monosomes was studied in detail with the objective of determining if irregular chromosome behavior (in addition to the univalent) was associated with quartet differences between monosomes. These results are presented in Table 12. (Fig. 3, Plate 4, shows the metaphase configuration of 19" 3').

No significant differences were demonstrated between Mono-VIII and Mono-XX or between Mono-XII and Mono-XXI which had counts of 34.3, 63.3, 40.4 and 44.9% of the quartets with micro-nuclei respectively.

Table 12

Metaphase Configuration of Monosomic Plants

Monosome studied	No. of plants examined	No. of count-able cells	Cells with		
			20" 1'	19" 3'	19" 3' in %
XII	5	473	458	15	3.2
XXI	4	324	318	6	1.9
VIII	5	257	238	19	7.4
XX	2	125	117	8	6.4

Plate 4

Chromosomes at Metaphase I

- Fig. 1. Normal, 21".
Fig. 2. Monosomic, 20" 1'.
Fig. 3. Monosomic, 19" 3'.
Fig. 4. Plant 15-H, 19" 2'.
Fig. 5. Plant 09-A, 20" 1' 1 fragment.

(Magnification 800 x)

Table 1

Summary of Results

1. Total number of cases	100
2. Number of cases with symptoms	75
3. Number of cases with signs	60
4. Number of cases with both symptoms and signs	45
5. Number of cases with neither symptoms nor signs	25

Metaphase I Measurement of Univalent Chromosomes

The mean lengths and widths of six monosomes at metaphase I are given in Table 13. A statistical analysis of the original micrometer readings showed that there were significant size differences between the univalent chromosomes. Comparisons were made using length and also the product of length x width. In both analyses, chromosome-XVIII was significantly smaller than all the others. No difference could be shown between chromosome-II and XII, or between XXI and VIII.

Table 13

Measurement of Monosomes at Metaphase I in Microns

Monosome studied	Plant 1		Plant 2		Plant 3		Mean	
	Length	Width	Length	Width	Length	Width	Length	Width
XXI	1.58	.40	1.56	.44	1.50	.48	1.55	.44
XX	1.48	.47	1.39	.49	1.54	.47	1.47	.48
XII	1.30	.45	1.47	.43	1.47	.43	1.41	.44
VIII	1.68	.46	1.52	.42	1.34	.46	1.51	.45
XVIII	1.18	.42	1.21	.40	1.20	.39	1.20	.40
II	1.42	.40	1.41	.43	1.44	.42	1.42	.42

 
9.	10.	11.	12.	13.	14.	15.	16.
 
33.	34.	35.	36.	37.	38.	39.	40.

Chromosomes at Anaphase I and Telophase I

The anaphase observations recorded in Table 14 show the various stages of normal and univalent chromosome movement that were thought to be most important. Because of the small number of counts and the error involved in classification, also the similarities of some classes, all results were examined on the basis of total counts.

In 165 cells in which the chromosomes could be clearly counted, none was found that had 21 chromosomes (20 dyads and one monad) at each pole. It can therefore be assumed from this count that the univalent often moves to the pole undivided. That each of the two daughter nuclei may eventually contain 20 dyads and one univalent chromatid is of course possible. The probability that the univalent which was lying in the centre (class No. 2) would split and pass poleward was indicated by classes 3 and 4. It can be safely assumed, however, that if the univalent does split, it does so after the bivalents have passed towards the poles. A partial split of the monosome was evident in some cells but the complete longitudinal separation and disjunction to the poles did not commence until after the bivalents disjoined. This characteristic behavior was observed even when it appeared that the univalent had orientated with the bivalents at metaphase. (Fig. 4, Plate 5). This indicates that the bivalents and the univalents behaved precociously and mitotically respectively.

Table 14

Distribution of Chromosomes at Anaphase I and Telophase I

Monosome studied	No. of plants	Classes						
		1	2	3	4	5	6	7
XII	4	30	19	68	23	12	1	5
VIII	5	29	10	68	13	10	3	3
XXI	4	26	13	67	25	5	2	2
XX	4	18	20	73	27	-	6	3
		—	—	—	—	—	—	—
	Total	103	62	276	88	27	12	13

Description of classes

1. 20 chromosomes at one pole, 21 at the other (Fig. 1, Plate 5).
2. 20 chromosomes at each pole with the univalent in the centre (Fig. 2, Plate 5).
3. Two daughter nuclei nearly formed with the univalent split and the two halves going to opposite poles (Fig. 3, Plate 6).
4. Two daughter nuclei nearly formed with the univalent split and the two halves going to the same pole (Fig. 4, Plate 6).
5. Two daughter nuclei nearly formed with the split univalent lying in the centre.
6. Fragmentated univalent (Fig. 2, Plate 6).
7. Other laggards besides the univalent lying between the two anaphasic chromosomes (Fig. 3, Plate 5).

Table 1

Summary of the results of the experiments conducted on the effect of the concentration of the solution on the rate of reaction.

Concentration of solution (M)	Time taken for reaction to complete (s)	Rate of reaction (1/s)
0.1	120	0.0083
0.2	60	0.0167
0.3	40	0.0250
0.4	30	0.0333
0.5	24	0.0417
0.6	20	0.0500
0.7	18	0.0556
0.8	15	0.0667
0.9	12	0.0833
1.0	10	0.1000

Graph of Rate of reaction vs. Concentration of solution

1. The rate of reaction increases as the concentration of the solution increases.
2. The rate of reaction is directly proportional to the concentration of the solution.
3. The rate of reaction is proportional to the square of the concentration of the solution.
4. The rate of reaction is proportional to the cube of the concentration of the solution.
5. The rate of reaction is proportional to the fourth power of the concentration of the solution.
6. The rate of reaction is proportional to the fifth power of the concentration of the solution.
7. The rate of reaction is proportional to the sixth power of the concentration of the solution.
8. The rate of reaction is proportional to the seventh power of the concentration of the solution.
9. The rate of reaction is proportional to the eighth power of the concentration of the solution.
10. The rate of reaction is proportional to the ninth power of the concentration of the solution.

Conclusion: The rate of reaction increases as the concentration of the solution increases.

Plate 5

Distribution of Chromosomes at Anaphase I

Fig. 1. 20--21.

Fig. 2. 20--20, with one univalent laggard.

Fig. 3. 19--20, with two univalent laggards in the centre.

Fig. 4. Bivalents divided, the univalent lagging at the metaphase plate.

(Magnification 800 X)

Table

Table 1. Results of the survey of the population of the city of Moscow in 1925.

1. Total population of the city of Moscow in 1925.	1,000,000
2. Population of the city of Moscow in 1920.	800,000
3. Population of the city of Moscow in 1915.	600,000
4. Population of the city of Moscow in 1910.	400,000
5. Population of the city of Moscow in 1905.	200,000

Plate 6

Univalent Chromosomes at Late Anaphase I

Fig. 1. Group of cells, some at interphase stage of division.

(Magnification 360 X)

Fig. 2. Fragmented univalent chromosome.

Fig. 3. Split univalent, chromatids "moving" to opposite poles.

Fig. 4. Split univalent, chromatids "moving" to the same pole.

(Magnification of Figs. 2, 3 and 4, 800 X)

The possibility of both halves of the univalent being included in one nucleus was indicated by class No. 4 where 23.4% of the cells show the chromatids going to one pole. If both were not included with the nucleus, the cell would have 2 micronuclei; if only one was included, a cell with 1 micronucleus would result.

Fragmentation of the univalent occurred in 12 or 3.2% of the telophase cells examined. Because of the position of the micronuclei in telo-interphase stages it was assumed that this fragmentation was the cause of at least some of the telo-interphase cells with 3-4 and 4 micronuclei. The difference in size of fragments was manifested in the size of the micronuclei.

The other laggards observed at anaphase I could partly be explained by tardy disjunction of bivalents. There were, however, cells in which it was definitely observed that the laggards resembled univalent chromosomes in that they had the characteristic longitudinal split into chromatids.

Other observations noted but not tabulated were:

1. appearance of only one partner of a split chromosome outside of the two daughter nuclei (Fig. 1, Plate 7),
2. appearance of a partially split chromosome, presumably being held together at the unsplit centromere, (Fig. 2, Plate 7),
3. Cells in which the dyads or univalents could not be counted but because there were no laggards it was assumed that a distribution of 21--20 had taken place.

In Plates 5, 6 and 7, some of the observations of anaphase I are illustrated.

Metaphase II and Anaphase II Observations

While paucity of material did not permit a thorough examination of chromosomes at metaphase II and anaphase II, several observations of these stages were recorded.

1. In many cells the univalent chromatids which had formed micronuclei in the first division failed to orientate at second metaphase. The micronuclei resolved into chromosomal structure but appeared to remain passive in the cytoplasm remaining in the same position that they occupied at the end of the first division (Fig. 1, Plate 8).
2. The split univalent chromosome was found with both chromatids in one cell or with one chromatid in each daughter cell, (Figs. 1 and 2, Plate 10).
3. Counts of chromosomes at anaphase II, indicated the possibility of having microspores with either 20 or 21 and even 22 chromosomes (Plate 9). In Fig. 5, Plate 9, because no micronuclei were present and the lower cell had 20 chromosomes at each pole, it was assumed that in each nucleus of the upper daughter cell there were 21 chromosomes.

 

4. Morphological and size differences existed among the chromosomes (Fig. 2, Plate 8).
5. Bridges or apparent bridges resulting from the stretching of a dicentric univalent were frequently formed (Fig. 3, Plate 9).
6. The misdivision of the univalent occurred more frequently at second division than at first division. In the majority of cells the fragmentation occurred in a definite place in the chromosomes. The likely point of breakage was at the centromere (Fig. 3, Plate 10).

the first of these is the fact that the

the second is the fact that the

the third is the fact that the

the fourth is the fact that the

the fifth is the fact that the

the sixth is the fact that the

the seventh is the fact that the

the eighth is the fact that the

Plate 7

Univalent Chromosomes at Late Anaphase I

Fig. 1. Split univalent, one chromatid not included in the daughter nuclei.

Fig. 2. Partially split univalent.

(Magnification 800 X)

Plate 8

Chromatids from the Univalent at Second Meiotic Division

Fig. 1. Metaphase II. Univalent chromatids have not orientated at the plate with the other chromosomes.

Fig. 2. Anaphase II. Size and morphology of the chromosomes.

(Magnification 500 X)

1947

1. General Information

1.1. Name of the project
1.2. Location of the project

1.3. Date of the project

(1.4. Other information)

1948

2. Objectives of the project

2.1. General objectives
2.2. Specific objectives

2.3. Methods of work

(2.4. Other information)

Plate 9

Distribution of the Chromosomes at Anaphase II

Fig. 1. 21--20, with one laggard.

Fig. 2. 20--20.

Fig. 3. 20--20 normal, 1 dicentric.

Fig. 4. 20--20, with one laggard.

Fig. 5. 20--20, presumed 21--21 in telophase daughter cell.

(Magnification of Figs. 1 - 4, 800 X; Fig. 5, 500 X).

Plate 10

Univalent Chromosomes at Late Anaphase II

- Fig. 1. Both chromatids of the univalent in one daughter cell.
Fig. 2. One chromatid of the univalent in each daughter cell.
Fig. 3. Fragmentation of chromatids from the univalent chromosome.

(Magnification 800 X)

(12-12-21)

THE PROGRESS OF THE WORK

1. The work done in the year 1921	1. 1
2. The work done in the year 1922	2. 1
3. The work done in the year 1923	3. 1

(12-12-21)

DISCUSSION AND CONCLUSIONS

The apparent irregularities among plants of a particular monosome for the formation of micronuclei in the quartets of microspores, observed in some of the preliminary and second counts, were an indication that some error was involved in classification. Counts of quartets from anthers of plants 97A-21 and 98A-2, showed that a random selection of anthers was unsatisfactory in the evaluation of the percentage of quartets having micronuclei. The greatest sources of error involved were:

- (a) the breaking up of quartets into dispersed microspores and
- (b) the loss of microcytes from the quartet arrangement.

Although there was some evidence that micronuclei were absorbed by the cytoplasm, the loss of micronuclei in this manner was too small to affect greatly the quartet counts. The variations caused by the above mentioned sources were eliminated when a critical stage was used.

It was confirmed by further counts that the regulating factor for the formation of micronuclei was uniformly active throughout the spike. The plants for which this uniformity was established were selected at random from the monosomic lines. While only nine plants were studied, it is reasonable to assume that this factor operated similarly in all plants of a monosome.

From the results of individual anther counts it was concluded that the force influencing formation of micronuclei was similar in different anthers of a floret. No evidence was found to support the theory (10) that variability existed within an anther. The regularity between plants of the same monosome for the formation of micronuclei in quartets showed that the forces or factors contributing to this formation were inherent within the particular monosome.

Sears (18) numbered the monosomes in the order in which he obtained them. They were designated I to XIV if belonging to the tetraploid series, and XV to XXI if they were in the C genome. From the compensating effect of Tetrasomic-II, Nullisomic-XX, and from phenotypic observations such as male and female sterility of monosomics and nullisomics, Sears (19) suggested possible homoeology between Mono-II, XX and XXIII. Similarly he postulated the association of Mono-VII, XI and XXI; VI, X and XIX; and III, XII and Mono-XVI. There is no statistical difference between the percentages of micronuclei observed for the monosomes of series 1 and 2. In the other suggested series no similarity between these chromosomes was indicated by the micronuclei count.

The limitations of this approach to a study of chromosome homologies and phylogeny were indicated by the estimations for the chromosomes in the C genome. The lowest value obtained

was 40% and in five of them over 50% of the quartets had micronuclei. Sears (19) has suggested that hexaploid wheat arose from a common progenitor. The process of evolution involved first, divergence into related genera, and then convergence through allopolyploidy into the present day hexaploid wheats. During the process of divergence and convergence the constitution of some chromosomes may have been altered more in one genome than in another. Whether the formation of micronuclei can be taken as an indicator of homology, is of course a matter of conjecture. Certainly one should not hesitate to associate two chromosomes even if counts between them are significantly different. Differences as large as 15 to 30% (and consistent differences) are, however, likely reflections of diverse material carried by such chromosomes.

If the formation of micronuclei were influenced by an internal force it would be expected that a correlation could be established between the number of micronuclei in the telo-interphase cells and in the quartets of microspores. This was demonstrated for only four of the six monosomes studied. However, the lack of great variability between counts of the same monosomic plants lends weight to the theory that some set force is operative for each chromosome. At the moment there appears to be no adequate explanation to account for the results obtained

for Mono-IV and Mono-XII. It may be that the force (or forces) acting on univalent chromosomes is not entirely similar at all phases of cell division for the different chromosomes. Consequently, frequency of micronuclei formation in the two stages studied may thereby be differentially affected.

One fact was clearly shown. There were more telo-interphase cells with one micronucleus than there were ⁱⁿ quartets. More misdivision or lagging of univalents occurred in the second division than in the first which would largely account for the difference. For all the monosomes the pattern for 3 micronuclei, 4 and over 4 micronuclei was very similar, in both the quartets and the telo-interphase cells.

The cause of different numbers of micronuclei per quartet should be briefly discussed.

Some possible sources of 1 micronucleus per quartet are:

1. complete failure of conjunction and disjunction of the univalent,
2. longitudinal division of the univalent at anaphase I and inclusion of only one chromatid at telophase II,
3. fragmentation at either first or second division and inclusion of all but one fragment.

Some possible sources of 2 micronuclei per quartet are:

1. longitudinal division at anaphase I and failure of inclusion of both chromatids at telophase II,
2. inclusion of one chromatid at second division but fragmentation of the daughter chromatid and failure of inclusion of both fragments,

3. fragmentation at either division and inclusion of all but 2 fragments.

Some possible sources of 3 micronuclei per quartet are:

1. longitudinal division at anaphase I and subsequent fragmentation of one chromatid at second division with all three portions being left out at telophase II,
2. bipartite fragmentation of both chromatids and inclusion of only 1 fragment,
3. fragmentation at first division of one chromatid and subsequent failure of inclusion of all three portions in second division.

A possible source of 4 micronuclei per quartet is:

1. bipartite fragmentation of univalent chromatids and exclusion of all fragments at telophase II.

The lagging caused by non-conjunction and non-disjunction of bivalents or univalents other than the monosomes (other laggards observed at anaphase I) could cause over 4 micronuclei per quartet. Such additional laggards could be responsible for various numbers of micronuclei, since they also could undergo fragmentation. Additional laggards present with the normal monosome could also cause the formation of one or more micronuclei in quartets.

The presence of five aberrations, other than the monosome, representing approximately 5% of the plants studied, suggests that the stability of the monosome may not be too great. Because micronuclei were observed in the quartets of these plants it also indicates that the presence or even the percentage of micronuclei as a criterion of the monosomic condition is not a completely reliable practice.

Myers and Powers (9) suggested that the frequency of formation of micronuclei may be a measure of the stability of a variety. The fairly high value obtained for Chinese Spring may be some indication of its lack of complete stability.

The micronuclei in normal 21 paired wheat must be the result of some weak pairing, predisjunction or non-conjunction of bivalents and univalents. Perhaps secondary pairing occurred between slightly homologous chromosomes of different genomes or even within genomes and thus unpaired univalents might be present.

No difference in frequency could be demonstrated between Mono-VIII and Mono-XX, regarding the metaphase configuration of 20" 1' and 19" 3'. There was no similarity regarding the percentage of micronuclei formed in these two chromosomes. It was therefore assumed that no connection existed between the frequency of 19" 3' observed and the percentage of micronuclei formed in quartets.

In plants with very small or numerous chromosomes it is often possible to use morphology as a character in the study of relationships. In T. vulgare there are three genomes and it may be possible to associate chromosomes or to distinguish each genome by morphological structure and size of the chromosomes. Differences in size of the univalents were demonstrated by metaphase I measurements. As shown by Fig. 2, Plate 8, the morphological difference between chromosomes is more apparent at anaphase II. A critical study in monosomic plants at this phase would possibly yield more information on chromosome homology if this is reflected by the chromosome size and morphology.

Some theories of chromosome movement involve the influence of the mass or physical condition of the chromosome. Sanchez-Monge (13) attributed the movement of the univalent to the metaphase plate to cytoplasmic currents. If mass has an effect on movement it is reasonable to assume that larger bodies might lag to a greater extent than smaller ones. From the measurements made at metaphase I, however, no correlation between size of monosomes and the number of micronuclei formed could be demonstrated.

The difficulty of interpreting results from fixed material is that the worker can only postulate the progressive behavior of the univalent from one stage to another by the

observations of the intermediate stages. From a study of anaphase I the following conclusions were made:

1. There is a definite cycle for bivalent orientation and disjunction and a definite cycle for univalents. The division of the univalent does not occur until after the bivalents have disjoined. Or in other words, the bivalents and univalents behave precociously and mitotically respectively.
2. The univalent moves towards the plate (presumably under the same orientation force to which bivalents are subjected) but often does not reach it before the phase of poleward movement is started.
3. If the univalent does not orientate the separation is usually not completed and the univalent moves to the nearest pole. If the univalent is near the metaphase plate and splitting when poleward movement sets in, both halves likely move to the same pole. One or both may be either included or left out of the nearest daughter nucleus. If the univalent orientates on the plate, splitting is completed and the halves pass towards opposite poles. Again one or both may fail to be included within the membrane of the daughter nucleus.

It is a very common mistake to suppose that the

following is a correct statement of the

principles of the theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

theory of the

4. Fragmentation from orientated or non-orientated univalents is possible and from observed constrictions the likely point of breakage is at the centromere.

After making allowances for sources of variability including personal error of observations and natural variations in plant material, it is clear that differences and similarities of behavior occurred among the 21 univalents of monosomic T. vulgare.

ACKNOWLEDGEMENTS

The author wishes to express his thanks and appreciation to Dr. J. Unrau, under whose guidance this study was conducted and the manuscript prepared; and to the National Research Council of Canada, for financial assistance in the form of a bursary.

REFERENCES

1. AASE, H. C. Cytology of Hybrids. Research Studies State Coll. Wash. 2:3-60. 1930.
2. FRANKEL, O. H. A self-propagating structural change in Triticum. Heredity 3:163-194. 1949.
3. GAJEWSKI, W. On the behavior of univalents at meiosis in some interspecific Geum hybrids. Hereditas 35:221-241. 1949.
4. HOWARD, H. W. Meiotic irregularities in hexaploid oats. J. Agr. Sci. 38:332-338. 1948.
5. HUSKINS, C. L. On the genetics and cytology of fatuoid or false wild oats. J. Genetics 18:315-363. 1927.
6. KAGAWA, F. and CHIZAKI, Y. Cytological studies on the genus hybrids among Triticum, Secale and Aegilops and the species hybrids in Aegilops. Japan J. Botany 7:1-32. 1934.
7. KIHARA, H. Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Ruecksicht auf das Verhalten der Chromosomen und die Sterilitaet in den Bastarden. Mem. Coll. Sci. Kyoto Imp. Univ. Ser. Bd. 1:1-200. 1924.
8. LOVE, R. M. Chromosome behavior in F₁ wheat hybrids. I. Pentaploids. Can. J. Research C,19:351-369. 1941.
9. MYERS, W. M. and POWERS, L. Meiotic instability as an inherited character in varieties of Triticum aestivum. J. Agr. Research 56:441-452. 1938.
10. POWERS, L. Cytological and genetic studies of variability of strains of wheat derived from interspecific crosses. J. Agr. Research 44:797-831. 1932.
11. _____ Cytological aberrations in relation to wheat improvement. J. Am. Soc. Agron. 24:531-536. 1932.

12. Proc. 5th Meet. Assoc. Comm. Plant Breed. Appendix R-U.
1950.
13. SANCHEZ-MONGE, E. Univalent mechanism and division.
An. Aula Dei 2(1):1-11. 1950.
14. _____ and MACKEY, J. On the origin of sub-
compactoids in Triticum vulgare. Hereditas
34:321-337. 1948.
15. SAX, K. Sterility in wheat hybrids. II. Chromosome be-
havior in partially sterile hybrids. Genetics
7:513-552. 1922.
16. _____ and SAX, H. J. Chromosome behavior in a genus
cross. Genetics 9:454-464. 1924.
17. SEARS, E. R. Cytogenetic studies with polyploid species
of wheat. I. Chromosomal aberrations in the
progeny of a haploid of Triticum vulgare. Gen-
etics 24:509-523. 1939.
18. _____ Cytogenetic studies with polyploid species
of wheat. II. Additional chromosomal aberrations
in Triticum vulgare. Genetics 29:232-246. 1944.
19. _____ The use of nullisomics in wheat genetics.
Proc. 5th Meet. Assoc. Comm. Plant Breed. Sub-
Appendix "a" 1-3. 1950.
20. SMITH, L. The acetocarmine smear technic. Stain Tech.
22:17-31. 1947.
21. SMITH, S. G., HUSKINS, C. L. and SANDERS, G. F. Mutations
in polyploid cereals. II. The cytogenetics of
speltoid wheats. Can. J. Research, C. 27:348-
393. 1949.
22. THOMPSON, W. P. Chromosome behavior in triploid wheat
hybrids. J. Genetics 17:43-48. 1927.
23. _____ and HOLLINGSHEAD, L. Preponderance of
dicoccum-like characters and chromosome numbers
in hybrids between T. dicoccum and T. vulgare.
J. Genetics 17:283-307. 1927.

 

24. UNRAU, J. The use of monosomes and nullisomes in cytogenetic studies of common wheat. Sci. Agr. 30:66-89. 1950.
25. VAARAMA, A. Cytological studies on some Finnish species and hybrids of the genus Rubus L. J. Sci. Agr. Soc. Finland 11:1-13. 1939.
26. WAKAR, B. A. Cytologische Untersuchung der ersten Generation der Weizenqueckenbastarde. Der Zuchter 7(8):199-206. 1935.