

MONOSOMIC ANALYSIS OF A CHLOROPHYLL DEFICIENCY

IN COMMON WHEAT

By

Fu-Sun Yen

A Thesis

Submitted to the Faculty of Graduate Studies

and Research in Partial Fulfilment

of the Degree of

Master of Science

University of Manitoba

1966



ACKNOWLEDGEMENTS

The writer wishes to express his gratitude to Dr. L. E. Evans, Department of Plant Science, for suggesting the problem, providing the materials, and for his advice and encouragement throughout the investigation.

Thanks are also extended to Dr. R. C. McGinnis and Dr. G.I. Paul for their suggestion in the preparation of the manuscript.

This project was made possible by financial grants from the National Research Council of Canada.

ABSTRACT

The inheritance of albinism in a Triticum durum line from the cross C.I. 8155 x Mindum⁴ was shown to be monogenic and recessive. Both green and albino seedlings were shown to have 28 chromosomes.

This character was transferred to hexaploid wheat by backcrossing to the variety Rescue and selecting segregating progeny after each backcross.

In this material it was found that albino seedlings had 40 chromosomes and green seedlings had from 40 to 42 chromosomes. Albino plants were found to be nullisomic for chromosome 3D which indicates that this chromosome carries a gene for chlorophyll production in the variety Rescue.

The study of F₂ lines from crosses between the hexaploid segregating lines and the Rescue monosomic series failed to reveal a critical chromosome in the A or B genome. There was some evidence however that homoeologous group III is probably involved.

Crosses between Vernal emmer and Marquis failed to produce albino offspring as reported by other authors.

TABLE OF CONTENTS

	<u>PAGE</u>
INTRODUCTION.....	1
LITERATURE REVIEW.....	3
MATERIALS AND METHODS.....	7
RESULTS AND DISCUSSION.....	10
GENERAL DISCUSSION AND CONCLUSIONS.....	32
REFERENCES.....	39

LIST OF TABLES

<u>TABLE</u>		<u>PAGE</u>
1.	Segregation in three Lethal Durum F ₅ lines.....	11
2.	The ratio of segregating and non-segregating lines in Lethal Durum F ₆ families..	12
3.	Segregation ratios in Lethal Durum F ₆ families.....	13
4.	The segregation ratios of 26 R ³ LD F ₂ lines.....	14
5.	The segregation ratios of seven cloned R ³ LD F ₃ lines.....	16
6.	The chromosome number and meiotic configurations of F ₁ hybrids of Rescue monosomics x R ³ LD lines with high albino frequencies.....	18
7.	The chromosome number and meiotic configurations of F ₁ hybrids of Rescue monosomics x R ³ LD lines with low albino frequencies.....	20
8.	Segregation in F ₂ seedlings from 39 and 40 chromosome F ₁ plants of Rescue monosomics x R ³ LD lines with high albino frequencies.....	24
9.	Segregation in F ₂ seedlings from 39 and 40 chromosome F ₁ plants of Rescue monosomics x R ³ LD lines with low albino frequencies.....	25
10.	Segregation in combined F ₂ lines from 39 and 40 chromosome F ₁ plants of Rescue monosomics x R ³ LD lines with high albino frequencies.....	27
11.	Segregation in combined F ₂ lines from 39 and 40 chromosome F ₁ plants of Rescue monosomics x R ³ LD lines with low albino frequencies.....	28
12.	Pollen transmission rate of the <u>n-1</u> gametes.....	30

LIST OF PLATES

<u>PLATE</u>		<u>PAGE</u>
I.	Figure 1. Green and albino Lethal Durum seedlings.....	35
	Figure 2. Nullisomic, monosomic and disomic F ₁ hybrids of Rescue monosomic 3D x R ³ LD.....	35
	Figure 3. Green and albino F ₂ seedlings of Rescue monosomics x R ³ LD.....	35
II.	Mitotic metaphase configurations of green and albino F ₂ seedlings of Rescue Monosomics x R ³ LD.....	36
III.	Meiotic configuration of double monosomic and nullisomic F ₁ Rescue monosomic x R ³ LD hybrids..	37
IV.	Figure 1. Green and albino F ₂ seedlings of Rescue monosomic 3D x R ³ LD.....	38
	Figure 2. Anaphase I of meiosis of an F ₁ double monosomic illustrating possible formation of <u>n-2</u> gametes	38

INTRODUCTION

During the past decade much progress has been achieved in the field of plant aneuploidy. Apart from the value of aneuploids as a genetic tool, their use in practical plant breeding is being explored. The production of aneuploid series, especially monosomics, in polyploid species of economic crops, has resulted in major advances in simplifying the analysis of polyploid inheritance, in locating genes on specific chromosomes and in analyzing chromosome translocations.

Abnormalities in the pattern of chlorophyll expression are not uncommon in the cereal grains and have been studied extensively, particularly those occurring as a result of mutation. In contrast to the number of chlorophyll mutations obtained in barley, chlorophyll mutations in hexaploid wheat are rare. Stadler (17) and others have concluded that radioinsensitivity of the chlorophyll system of hexaploid wheat is primarily due to gene duplication.

Although chlorophyll deficiencies affect populations adversely, they are very useful to the geneticist. They supply easily identifiable loci for chromosome mapping and make excellent markers for studying the effects of various mutagenic agents on mutation frequency in many plants. Chlorophyll-deficient seedling characters may be used to identify and characterize a population. They also enable the geneticist to make inferences relative to types of

gene action and the selective advantage of homozygotes versus heterozygotes.

Philp (5) pointed out that polymeric genes (V genes) are responsible for chlorophyll production and that at least two and probably three loci are involved in chlorophyll production in Avena sativa. McGinnis and associates (8, 9, and 10) have located two genes, V₁ and V₂ for chlorophyll production on chromosomes 15 and 21 respectively, through karyotype analysis and aneuploid studies in Avena sativa.

The object of the present project was to study the inheritance of albinism in a strain of Triticum durum and to determine by means of monosomic analysis the chromosomes involved in the control of this character when it is transferred to hexaploid wheat.

LITERATURE REVIEW

I. CHLOROPHYLL DEFICIENCIES IN OATS

The first reports of albinism in common oats were by Nilsson-Ehle in 1913 and by Akerman in 1922. The latter observing them in hybrids of a Swedish black-hulled variety and the variety Probesteier (reported by Froier (3)).

Philp (5) studying the cytogenetics of albino oats found that albino seedlings had only 40 chromosomes, whereas the parent plants of albinos were monosomic.

McGinnis and associates (8, 9, and 10) have identified chromosomes 15 and 21 of Avena sativa as having genes for chlorophyll production and inferred that a third locus is probably involved since Avena sativa is an allohexaploid.

II. CHLOROPHYLL-DEFICIENCIES IN WHEAT

Froier (3) reported that Meister (1922) obtained albinos from a cross of Triticum durum x T. vulgare and that Vavilov and Jakushkina (1925) found that chlorophyll-deficient plants were produced from crosses between T. vulgare v. lutescens Al. and T. dicoccum v. pycnurum. They also obtained only albino F₁ seedlings from the cross T. durum v. melanopus Al. x T. spelta No.25.

Harrington and Smith (4) reported that in the F₂ generation of a cross between Khapli and Early Emmer, approximately one-sixteenth of the seedlings were bright

yellow in color. When grown in the greenhouse, the yellow seedlings developed some chlorophyll. The results showed that two recessive genes, designated a and b, for the inhibition of chlorophyll development are carried by Khapli and Emmer respectively. When these genes are present in the homozygous condition, the seedlings are yellow.

According to Froier (3), Khintshuk (1929) examined the chlorophyll mutants, albina, xantha and flavescens, in the F₃ and F₄ generations from the cross of Triticum timopheevi Zhuk. var. viticulosum and T. persicum Vav. and suggested that two factors were responsible for chlorophyll production.

Smith and Harrington (16) reported that in the F₂ generation of a cross between Vernal emmer (C.I. 3686) (T. dicoccum) and Marquis (T. vulgare) approximately one sixty-fourth of the seedlings were albinos. They suggested that one parent carries two recessive genes for albinism which are complementary to a third gene carried by the other parent. These three genes when present together in the homozygous recessive condition inhibit the development in chlorophyll.

Froier (3) cited that L. A. Sapehin (1932) reported two factor pairs were responsible for albinism and two factor pairs were responsible for yellow seedlings in T. durum crosses. From crosses between T. durum and

T. dicoccum, he concluded that three factor pairs controlled the albinism.

A mutable recessive gene that causes a virescent condition in Triticum aestivum was reported by Neatby in 1933 (11).

Froier (3) reported that Kihara (1937) found chlorophyll mutants from hybrids of Triticum persicum v. stramineum and T. timopheevi. He concluded that yellow seedlings (xantha or lutescens) were homozygous for one recessive gene *y*. Seedlings with two recessive genes, *a*₁ and *a*₂ were albinos.

Chromosomes of homoeologous group III of common wheat have been shown by Sears (14) to affect chlorophyll formation. Steinitz-Sears (18) found that the gene *v* (virescent) is located on the short arm of chromosome 3B.

III. PECULIARITIES OF MONOSOMIC OR NULLISOMIC 3D LINES OF COMMON WHEAT

A line of wheat nullisomic for chromosome 3D (XVI) was discovered in the F₅ generation of the pentaploid hybrid Rescue x Golden Ball by Larson (6). A study of chlorophyll turnover and of the products of photosynthesis by means of radioactive tracers in this nullisomic 3D wheat was investigated by Larson and Perkins (7). They found that the nullisomic had a ratio of labelled carotenes to xanthophylls different from that of the other varieties,

and it resembled Golden Ball in having a high amount of C^{14} in the hot water-soluble extract. They suggested that the differences between the nullisomic and the two hexaploid wheats were probably due to the loss of chromosome 3D (7).

Bhowal (1) found an unusual segregation of disomics, monosomics, and nullisomics in the offspring of a substitution of Rescue x Golden Ball. Pollen with 20 and 21 chromosomes occurred in the frequency of 64 and 36%, respectively. The 61% transmission of the deficiency on the male side and 76% on the female explained the unusual segregation in the summer crop. Bhowal (2) also found that normal pollen with chromosome 3D from Red Bobs has little competitive advantage over pollen deficient for chromosome 3D, when a substituted monosomic line of wheat derived from the hybrid Rescue x Golden Ball was selfed.

MATERIALS AND METHODS

The material utilized included:

(I) Lethal Durum - This is a line obtained from an F_3 plant of the cross C.I. 8155 x Mindum⁴ which segregated to produce albino seedlings (shown in Plate I, Figure 1). This stock was produced and supplied by Dr. E. R. Kerber, C.D.A., Winnipeg.

(II) Rescue³ Lethal Durum (R^3LD) is a segregating line derived from crossing Rescue (Triticum aestivum) to Lethal Durum and backcrossing twice to Rescue. Following the second backcross 26 of 41 F_1 plants produced segregating F_2 progeny. These 26 lines were utilized in this study.

(III) The Rescue monosomic series produced by Dr. R. I. Larson, C.D.A., Lethbridge.

(IV) The T. aestivum variety Marquis and the emmer variety Vernal.

Three segregating F_5 lines of Lethal Durum were studied to check the assumption that a single recessive factor conditioned albinism. F_6 lines derived from single F_5 plants were also grown and examined.

Study of the 26 segregating R^3LD lines revealed differences in their segregation ratios and on this basis four with a high albino frequency and three with a low frequency were selected. Six to eight plants from each of the seven lines were cloned. One clone of each plant was grown in the greenhouse and was selfed. The remaining clones of

each plant were maintained in a cold room at 38-42°F. The selfed seeds from the greenhouse grown clones were germinated and the segregation ratio in each progeny recorded. The remaining clones of plants which the progeny test showed to be segregating were used as pollen parents to cross with the 21 Rescue monosomic lines, the high and low frequency groups being used as separate bulk pollen sources. Root tips were collected from all plants in segregating progenies and chromosome numbers determined at mitotic metaphase using the Feulgen method.

Due to the fact that albino seedlings had 40 chromosomes and that green seedlings varied from 40 to 42 chromosomes, monosomic R³LD plants from the lines with both high and low albino frequencies were crossed to normal Rescue to determine the n-1 male gamete transmission rate.

The F₁ seeds from the crosses of the Rescue monosomics x R³LD were germinated and chromosome numbers were determined for all plants at mitotic metaphase. Four hundred and eighty-one F₁ seedlings of Rescue monosomics x R³LD high frequency lines and 498 F₁ seedlings of Rescue monosomics x R³LD low frequency lines were grown and checked for chromosome number.

Spikes from F₁ plants with 40 or 39 chromosomes were collected and fixed in Carnoy's Fluid (6:3:1, alcohol,

chloroform and acetic acid) and analysed at metaphase I of meiosis. All F_2 seeds from such plants were germinated and the segregation ratios and chromosome numbers determined. The F_2 seeds from 70 F_1 plants of Rescue monosomics x R^3LD with 42 chromosomes were likewise analysed.

In an attempt to identify the chromosome involved in the A or B genome, 15 green F_2 plants with 39 or 40 chromosomes from double monosomics (4A, 3D) and (3B, 3D) and seven nullisomic 3D plants from selfed monosomic R^3LD were planted in the greenhouse. The nullisomic 3D plants were used as both female and male parents to cross with F_2 plants from double monosomics (4A, 3D) and (3B, 3D).

Reciprocal crosses of Marquis x Vernal emmer were made. The root tips of each F_1 hybrid were collected and counted. Some F_1 plants were selfed and the remainder were backcrossed to Marquis. The root tips of F_2 and backcrossed F_1 seedlings were collected. F_3 seeds and a large sample of backcrossed F_2 seeds were germinated in the germination boxes to examine the color of seedlings.

RESULTS AND DISCUSSION

I. THE MODE OF INHERITANCE IN LETHAL DURUM

The segregation ratios for the three F₅ lines are included in Table 1. All approximated a ratio of 3 green to 1 albino as do the pooled results. This would indicate that albinism is monogenically controlled.

The green plants of each F₅ line were selfed to produce seed for F₆ families. It was expected that 1/3 of the families would breed true and 2/3 segregate. The data in Table 2 agrees with the expected frequencies.

Table 3 summarizes the segregation occurring in each segregating F₆ family. All fit the theoretical expectation but a significant homogeneity χ^2 is attained for family 1. On the basis of all the data, however, it is apparent that the occurrence of albino seedlings in the Lethal Durum strain is simply inherited and due to the homozygous recessive condition.

A total of 89 green and 21 albino seedlings were cytologically examined and all had a 2n number of 28.

II. RESCUE³ LETHAL DURUM

The segregation in each of the 26 R³LD F₂ lines is presented in Table 4. Those selected as the low frequency group included 1-2, 1-3, and 1-6 while the high frequency group included 1-9, 3-12, 3-13 (progeny test showed high

TABLE 1.
 SEGREGATION IN THREE LETHAL DURUM F₅ LINES

Lethal Durum F ₅ Line	Number of Seedlings		X ² -Value (3:1)	Probability
	Green	Albino		
No.1	21	4	1.08	0.25-0.50
No.2	17	8	0.65	0.25-0.50
No.3	15	8	1.17	0.25-0.50
Totals	53	20	0.22	0.50-0.75

TABLE 2.

THE RATIO OF SEGREGATING AND NON-SEGREGATING
LINES IN LETHAL DURUM F₆ FAMILIES.

Lethal Durum F ₆ Family	Observed		Expected (1:2)		χ ² -Value (1:2)	Probability
	Non-segregating Lines	Segregating Lines	Non-segregating Lines	Segregating Lines		
1	4	8	4	8	0	1
2	7	9	5.33	10.67	0.78	0.25-0.50
3	7	10	5.67	11.33	0.47	0.25-0.50

TABLE 3

SEGREGATION RATIOS IN LETHAL DURUM F₆ FAMILIES

Line	Number of Seedlings			X ² - Value (3:1)	Probability
	Green	Albino	Total		
1- 2	17	1	18	2.6667*	0.10-0.25
1- 3	7	5	12	1.7778	0.10-0.25
1- 4	11	7	18	1.8519	0.10-0.25
1- 5	4	5	9	3.0000*	0.05-0.10
1- 6	6	1	7	0.4286	0.50-0.75
1- 8	9	2	11	0.2727	0.50-0.75
1- 9	14	1	15	1.8000*	0.10-0.25
1-10	15	2	17	0.9608*	0.25-0.50
Totals	83	24	107		
2- 2	17	7	24	0.2222	0.50-0.75
2- 3	18	6	24	0	1
2- 4	15	5	20	0	1
2- 7	14	1	15	1.8000*	0.10-0.25
2- 8	16	8	24	0.8889	0.25-0.50
2-10	11	3	14	0.0952	0.75-0.90
2-12	18	5	23	0.1304	0.50-0.75
2-14	12	4	16	0	1
2-18	11	3	14	0.0952	0.75-0.90
Totals	132	42	174	4.1208(9df) 0.0690(1df)	
3- 1	17	6	23	0.0145	0.90
3- 3	19	11	30	2.1778	0.10-0.25
3- 5	16	3	19	0.8305	0.25-0.50
3- 8	10	3	13	0.0256	0.75-0.90
3-10	19	5	24	0.2222	0.50-0.75
3-11	11	5	16	0.3333	0.50-0.75
3-14	17	4	21	0.3968	0.50-0.75
3-15	21	5	26	0.4615	0.25-0.50
3-16	20	4	24	0.8889	0.25-0.50
3-19	19	5	24	0.2222	0.50-0.75
Totals	169	51	220	5.5733(10 df) 0.3879(1 df)	

* Adjusted X²-value

Family 1: homogeneity X² = 16.3422 with 7 df. P = 0.025-0.01

Family 2: homogeneity X² = 4.0523 with 8 df. P = 0.75-0.90

Family 3: homogeneity X² = 5.2144 with 9 df. P = 0.75-0.90

TABLE 4
 THE SEGREGATION RATIOS OF 26 R³LD F₂ LINES

Line	Number of Seedlings	
	Green	Albino
1- 2	53	3
1- 3	106	8
1- 6	92	7
1- 9	64	27
2- 1	64	13
2- 2	35	13
2- 3	24	17
2- 6	17	10
2- 7	34	21
2- 9	23	6
2-10	10	9
2-11	21	7
2-12	20	15
2-13	24	8
3- 2	37	17
3- 4	25	17
3- 5	18	10
3- 6	12	8
3- 9	29	24
3-10	54	30
3-11	59	23
3-12	37	9
3-13	13	1
3-14	41	19
3-15	36	15
3-16	47	10



frequency), and 3-16. The three segregating lines in the low frequency group gave an overall ratio of 251 green: 18 albino seedlings whereas the high frequency (except line 3-13) total was 148 green to 46 albinos, or frequencies of 6.7% and 23.8% albinos respectively.

A total of 43 plants from these seven lines were cloned with one clone of each plant being grown rapidly to maturity while the remaining clones were maintained at 38-42°F until the segregation could be determined so that only heterozygous plants were used as pollen parents. Of the 43 plants two failed to survive, of the remaining 41 plants 18 were found to be heterozygous as evidenced by segregation in the seedlings derived from the greenhouse grown clones.

The segregation occurring in the progeny of each of these 18 plants is shown in Table 5. The seven lines in the low frequency group gave an overall ratio of 447 green: 35 albino seedlings whereas the high frequency total was 215 green to 45 albinos, or frequencies of 7.3% and 17.3% albinos respectively.

The chromosome numbers of the green and albino seedlings in the segregating progeny were checked and all the albinos had 40 chromosomes whereas the green seedlings had from 40 to 42 chromosomes. On this basis the segregation ratios occurring in the lines shown in Tables 4 and

TABLE 5
 THE SEGREGATION RATIOS OF SEVEN CLONED R³LD F₃ LINES

R ³ LD F ₃ Line	Number of Seedlings	
	Green	Albino
1- 2-1	26	1
1- 2-3	37	2
1- 2-4	56	3
1- 2-6	40	1
1- 3-2	65	1
1- 3-3	77	2
1- 3-5	36	18
1- 3-8	60	1
1- 6-1	10	2
1- 6-4	39	3
1- 6-6	1	1
1- 9-1	24	5
1- 9-3	15	11
3-12-1	43	6
3-12-2	37	14
3-13-1	14	6
3-16-1	43	3
3-16-3	39	6

and 5 result from both genic segregation and chromosome number differences. This situation is very similar to that reported in Avena sativa by McGinnis and associates (8, 9 and 10). There are two possible explanations for these results; either the 40 chromosome albino plants were nullisomic and green 40 chromosome plants double monosomics or else all 40 chromosome plants were nullisomic and segregation occurred at a second locus. The fact that the frequency of albinos in these two groups was 6.7% and 23.8% respectively supports the latter theory. The high frequency monosomic group could be designated as aaB - wherein all 40 chromosome nullisomics would be aa-- and albino while the low frequency group could be designated AaB-, wherein $\frac{1}{4}$ of the nullisomics would be albino thus agreeing with the above frequencies.

III. THE F₁ HYBRIDS OF THE RESCUE MONOSOMICS X R³LD

All F₁ seedlings from the crosses between the Rescue monosomics and R³LD were checked for chromosome number. The data are summarized in Tables 6 and 7. From male parents with high albino frequency, the number of F₁ plants with 42, 41 and 40 (including 39) chromosomes was 112, 304 and 65 or 23.28%, 63.2% and 13.51% respectively. From male parents with low albino frequency, the number of F₁ plants with 42, 41 and 40 (including 39) chromosomes was 123, 324 and 51 or 24.7%, 65.06% and 10.24% respectively. The

TABLE 6

THE CHROMOSOME NUMBER AND MEIOTIC CONFIGURATIONS OF F₁ HYBRIDS OF
RESCUE MONOSOMICS X R³LD LINES WITH HIGH ALBINO FREQUENCIES

F ₁ Line	Number of Seedlings	Chromosome Number and Meiotic Configuration				
		42	41	40	39	
		19 ^{II} +2 ^I &/or 18 ^{II} +4 ^I	19 ^{II} +1 ^I &/or 18 ^{II} +3 ^I	20 ^{II}	19 ^{II} +1 ^I &/or 18 ^{II} +3 ^I	
R1A x R ³ LD	26	1	23	2		
R2A x R ³ LD	14	2	10	2		
R3A x R ³ LD	18	7	9	2		
R4A x R ³ LD	24	14	10			1
R5A x R ³ LD	32	5	21	5		
R6A x R ³ LD	45	9	28	8		
R7A x R ³ LD	38	4	30	4		
R1B x R ³ LD	26	3	19	3		1
R2B x R ³ LD	7		6	1		
R3B x R ³ LD	6	1	4	1		
R4B x R ³ LD	24	6	13	4		1
R5B x R ³ LD	32	10	21	1		
R6B x R ³ LD	31	3	24	3		1
R7B x R ³ LD	29	4	20	5		
R1D x R ³ LD	30	17	12	1		
R2D x R ³ LD	10	5	2	3		

continued

TABLE 6 CONTINUED

F ₁ Line	Number of Seedlings	Chromosome Number and Meiotic Configuration			
		42	41	40	39
			19 ^{II} +2 ^I &/or 18 ^{II} +4 ^I	20 ^{II}	19 ^{II} +1 ^I &/or 18 ^{II} +3 ^I
R3D x R ³ LD	9		8		1
R4D x R ³ LD	10	4	2	4	
R5D x R ³ LD	39	7	26	6	
R6D x R ³ LD	19	5	11	3	
R7D x R ³ LD	12	5	5	2	
Totals	481	112	304	60	1
					4

TABLE 7

THE CHROMOSOME NUMBER AND MEIOTIC CONFIGURATIONS OF F₁ HYBRIDS OF
 RESCUE MONOSOMICS X R³LD LINES WITH LOW ALBINO FREQUENCIES.

F ₁ Line	Number of Seedlings	Chromosome Number and Meiotic Configuration			
		42	41	40	39
		19 ^{II} +2 ^I &/or 18 ^{II} +4 ^I	20 ^{II}	19 ^{II} +1 ^I &/or 18 ^{II} +3 ^I	-
R1A x R ³ LD	39	6	28	5	
R2A x R ³ LD	4	2	2		
R3A x R ³ LD	25	7	16	2	
R4A x R ³ LD	18	7	10	1	
R5A x R ³ LD	27	6	18	3	
R6A x R ³ LD	19	4	13	2	
R7A x R ³ LD	29	2	25	2	
R1B x R ³ LD	21	4	17		
R2B x R ³ LD	23	6	15	2	
R3B x R ³ LD	30	12	17	1	
R4B x R ³ LD	41	11	25	5	
R5B x R ³ LD	24	7	12	3	2
R6B x R ³ LD	12	2	8	1	1
R7B x R ³ LD	21	6	13	2	
R1D x R ³ LD	29	20	9		
R2D x R ³ LD	43	4	30	8	1

TABLE 7 CONTINUED

F ₁ Line	Number of Seedlings	Chromosome Number and Meiotic Configuration			
		42	41	40	39
		19 ^{II} +2 ^I &/or 18 ^{II} +4 ^I	19 ^{II} +1 ^I &/or 18 ^{II} +3 ^I	20 ^{II}	19 ^{II} +1 ^I &/or 18 ^{II} +3 ^I
R3D x R ³ LD	18	3	13		2
R4D x R ² LD	27	2	22	3	
R5D x R ³ LD	14	8	5	1	
R6D x R ³ LD	28	1	23	4	
R7D x R ³ LD	6	3	3		
Totals	498	123	324	45	2
					4

difference between these two groups is not significant ($t = 0.56$ with 2 df.). χ^2 -test for independence showed that there is no association between chromosome number and transmission frequency in the segregating populations ($\chi^2 = 2.8251$ with 2 df., $P = 0.1 - 0.25$.) This indicates that the male transmission of $n-1$ gametes does not differ between the high and low albino frequency groups and that the difference in albino frequency is genic and not chromosomal.

The meiotic configuration of each F_1 plant with 40 or 39 chromosomes was examined. For those F_1 plants with 40 chromosomes, a configuration of 20 bivalents at metaphase I would indicate that the plant was nullisomic, but 19 bivalents plus 2 univalents would indicate that they were double monosomics. A total of 137 F_1 plants which included plants derived from each of the 21 monosomic lines, were examined at metaphase I of meiosis (Tables 6 and 7). Three plants of Rescue monosomic 3D x R^3 LD with 40 chromosomes had a meiotic configuration of 20 bivalents. Forty chromosome plants from the other 20 lines all had meiotic configurations of 19 bivalents plus 2 univalents (shown in Plate III). This proves that the missing chromosome in monosomic R^3 LD is chromosome 3D.

The fact that no albino F_1 plants were obtained indicates that Rescue must have a genotype differing from

R³LD. Rescue probably carries an allele dominant to the recessive gene transferred to R³LD from Lethal Durum.

The nullisomic, monosomic and disomic 3D F₁ plants of the Rescue monosomic x R³LD are shown in Plate I, Figure 2. The phenotypic characteristics of nullisomic 3D were the same as Chinese Spring nullisomic 3D which Sears (13) described as having short culms, narrow leaves, and short, very dense spikes, frequently bent and twisted.

The occurrence of eight 39 chromosome plants probably indicates that n-2 gametes also occasionally function in the R³LD male parents. The transmission of deficient male gametes by R³LD rendered the 41 chromosome F₁ plants useless in that they could not be identified as to the missing chromosome. Therefore the progeny of 40 chromosome F₁ plants were analyzed in an attempt to identify critical lines other than 3D.

IV. F₂ LINES FROM 39 AND 40 CHROMOSOME F₁ PLANTS

The segregation ratios in the F₂ seedlings are presented in Tables 8 and 9. The chromosome numbers of the progeny ranged from 39 to 42 with all albino plants having either 39 or 40 chromosomes (shown in Plate I, Figure 3 and Plate II). From a total of 4240 F₂ seeds produced 423 failed to germinate. These may be zygotic lethals that should rightfully be recorded in the albino class.

SEGREGATION IN F₂ SEEDLINGS FROM 39 AND 40 CHROMOSOME F₁ PLANTS OF
RESCUE MONOSOMICS X R³LD LINES WITH HIGH ALBINO FREQUENCIES

F ₂ Line of Rescue Monosomics x R ³ LD	Chromosome		Number of Seedlings		Un- germinated Seeds	Total Number	Number of Counted Seedlings					
	Number of F ₁ Plants		Green	Albino			Green Chromosome Number				Albino Chromosome Number	
	40	39					42	41	40	39	40	39
R1A x 1-9-1F ₂ -1	x		78	3	3	61	2	6	40	10		3
R1A x 1-9-1F ₂ -2	x		50	2	5	16		5	7	3		1
R1A x 3-12-1F ₂ -1	x		3	3	0							
R1A x 3-12-1F ₂ -15	x		27	0	2							
R2A x 1-6-1F ₂ -1	x		114	0	4	14	4	5	4	1		
R2A x 3-13-1F ₂ -2	x		1	0								
R3A x 1-3-5F ₂ -11	x		2	0		2		2				
R5A x 1-3-5F ₂ -2	x		91	4	30	26	1	4	16	1	2	2
R5A x 1-3-5F ₂ -9	x		51	4	25	11	1	3	3	1	3	
R5A x 3-12-2F ₂ -4		x	16	0								
R5A x 3-12-2F ₂ -6	x		6	0								
R5A x 3-12-2F ₂ -9	x		13	2								
R5A x 3-12-2F ₂ -10	x		16	3	1							
R6A x 1-3-5F ₂ -1	x		93	2	20	30		5	22	1	2	
R6A x 1-3-5F ₂ -6	x		55	6	6	12		2	4	1	1	4
R6A x 1-3-5F ₂ -7	x		34	2	3	6		3		1	1	1
R6A x 3-12-1F ₂ -12	x		28	0								
R6A x 3-12-1F ₂ -5	x		33	0	16	2		1	1			
R6A x 3-13-1F ₂ -6	x		17	0		3			2	1		
R6A x 3-16-3F ₂ -1	x		26	0	5							
R7A x 1-9-1F ₂ -2	x		12	2	0	6			4		2	
R7A x 3-12-2F ₂ -5	x		61	1	11	5	1	1	2		1	
R1B x 3-13-1F ₂ -3	x		54	0								
R1B x 3-13-1F ₂ -4		x	6	0								
R1B x 3-13-1F ₂ -6	x		98	0	1							
R1B x 3-16-1F ₂ -6	x		27	0	10							
R2B x 3-12-2F ₂ -1	x		43	0	2							
R3B x 1-3-5F ₂ -1	x		14	3	2	17		4	8	2		3
R4B x 1-6-1F ₂ -4		x	9	0	2	1		1				
R4B x 1-6-1F ₂ -5	x		25	4	5	4	1	1			1	1
R4B x 1-6-1F ₂ -6	x		69	0	9	9	2	1	3	3		
R4B x 1-6-1F ₂ -8	x		26	0		4	1	1	2			
R6B x 3-12-1F ₂ -5	x		68	0								
R6B x 3-16-1F ₂ -2	x		13	0	5							
R6B x 3-16-3F ₂ -2	x		23	0								
R7B x 1-9-1F ₂ -1	x		89	11	20	40	3	7	16	4	6	4
R7B x 3-12-1F ₂ -9	x		20	1	3							
R7B x 3-12-1F ₂ -10	x		50	0								
R7B x 3-12-1F ₂ -15	x		31	3	6							
R1D x 3-13-1F ₂ -4	x		39	3	14	14		8	3	1	2	
R2D x 3-12-1F ₂ -1	x		14	0								
R2D x 3-13-1F ₂ -6	x		62	0	24	26	4	11	10	1		
R3D x 1-9-3F ₂ -2	x		6	3	1	9		1	5		2	1
R4D x 1-6-1F ₂ -3	x		31	0		4		1	3			
R4D x 1-6-1F ₂ -6	x		99	1	15	6		4	1	1		
R4D x 1-6-1F ₂ -8	x		84	0	7	4		2	2			
R4D x 1-6-1F ₂ -9	x		40	1	6	2			2			
R5D x 1-3-5F ₂ -5	x		56	8	17	22		5	7	3	6	1
R5D x 3-12-1F ₂ -3	x		19	3	5							
R5D x 3-12-1F ₂ -7	x		10	3	1							
R5D x 3-12-1F ₂ -11	x		36	0								
R5D x 3-12-1F ₂ -19	x		21	0								
R5D x 3-12-1F ₂ -24	x		11	2	1							
R6D x 3-12-1F ₂ -7	x		18	0								
R6D x 3-12-2F ₂ -5	x		35	1		1					1	
R6D x 3-12-2F ₂ -9	x		52	3	1	7		1	3		1	2
R7D x 1-6-1F ₂ -2	x		10	0								
R7D x 3-12-1F ₂ -1	x		24	2	14							
Totals			2193	83	302							

TABLE 9

 SEGREGATION IN F₂ SEEDLINGS FROM 39 TO 40 CHROMOSOME F₁ PLANTS OF
 RESCUE MONOSOMICS X R³LD LINES WITH LOW ALBINO FREQUENCIES

F ₂ Line of Rescue Monosomics x R ³ LD	Chromosome Number of F ₁ Plants		Number of Seedlings		Un- germinated Seeds	Total Number	Number of Counted Seedlings												
	40	39	Green	Albino			Green				Albino								
							Chromosome Number	Chromosome Number	42	41	40	39	40	39					
R1A x 1-3-8F ₂ -6	x		16	0	1														
R1A x 1-3-8F ₂ -15	x		6	0															
R1A x 1-3-8F ₂ -16	x		7	1															
R4A x 1-2-6F ₂ -16	x		18	5	2	23	1	6	7	4		1	4						
R5A x 1-2-1F ₂ -9	x		60	0															
R5A x 1-3-8F ₂ -12	x		47	0															
R6A x 1-2-6F ₂ -1	x		19	1															
R6A x 1-2-6F ₂ -5	x		46	0															
R7A x 1-2-1F ₂ -3	x		39	0															
R7A x 1-2-6F ₂ -7	x		23	0															
R2B x 1-2-6F ₂ -1	x		8	0	1														
R2B x 1-3-3F ₂ -1	x		60	0	1														
R2B x 1-3-8F ₂ -8	x		7	1	1														
R4B x 1-2-1F ₂ -4	x		40	0	2														
R4B x 1-2-6F ₂ -6	x		31	0															
R4B x 1-2-6F ₂ -7	x		5	0															
R4B x 1-2-6F ₂ -23	x		29	0															
R4B x 1-3-2F ₂ -1	x		16	3															
R4B x 1-6-4F ₂ -1	x		18	0															
R5B x 1-3-2F ₂ -2		x	25	1	11														
R5B x 1-3-2F ₂ -12		x	11	1	5														
R5B x 1-3-2F ₂ -13	x		23	1	13														
R5B x 1-3-2F ₂ -18	x		43	6	9														
R5B x 1-3-8F ₂ -3	x		34	9	6														
R5B x 1-3-8F ₂ -4	x		18	0	2														
R6B x 1-2-1F ₂ -5	x		18	0															
R6B x 1-2-1F ₂ -6	x		25	0															
R6B x 1-6-4F ₂ -5		x	25	0	1														
R7B x 1-2-6F ₂ -2	x		26	0	1														
R7B x 1-3-3F ₂ -2	x		6	0															
R7Bx 1-6-4F ₂ -5	x		55	0															
R2D x 1-2-1F ₂ -1	x		27	0															
R2D x 1-2-1F ₂ -4	x		35	0	4														
R2D x 1-2-1F ₂ -5	x		29	6	1														
R2D x 1-2-1F ₂ -6	x		10	0	3														
R2D x 1-2-6F ₂ -2	x		24	0															
R2D x 1-2-6F ₂ -11	x		22	0															
R2D x 1-3-2F ₂ -2	x		21	0	5														
R2D x 1-3-2F ₂ -10	x		24	0	1														
R2D x 1-6-4F ₂ -5		x	55	0	1														
R3D x 1-3-8F ₂ -7		x	36	3	4	23	2	15	5	1									
R4D x 1-2-6F ₂ -2	x		12	2	3														
R4D x 1-2-6F ₂ -17	x		56	0	1														
R4D x 1-2-6F ₂ -27	x		14	2	1														
R4D x 1-2-6F ₂ -33	x		21	0	3														
R5D x 1-2-1F ₂ -1	x		22	0	1														
R5D x 1-2-1F ₂ -6	x		15	1															
R5D x 1-2-6F ₂ -7	x		32	3	2														
R6D x 1-3-2F ₂ -6	x		27	1	5														
R6D x 1-3-2F ₂ -11	x		19	1	2														
R6D x 1-3-2F ₂ -12	x		52	3	14														
R6D x 1-3-2-F ₂ -20	x		73	0															
R6D x 1-6-4F ₂ -3	x		59	1	14														
Totals			1489	52	121														

Since the 40 chromosome F_1 plants that gave rise to these F_2 progeny were double monosomics, then the non-critical F_1 genotypes could be designated $AaB-$ and the critical as $a-B-$ from high albino frequency males and $A-B-$ and $a-B-$ in equal frequency from the low albino frequency males.

In the case of the high frequency population the frequency of albino 40 chromosome plants should be three times as great in the critical as in the non-critical lines assuming the frequency of nullisomic 3D plants is equal in each line.

On this basis the segregation ratio for each F_2 line from high and low albino frequencies was combined. These data are summarized in Tables 10 and 11. It has been shown that the missing chromosome in monosomic R^3LD is chromosome 3D which carries a gene for chlorophyll production. The albinism in Lethal Durum is monogenic. The gene transferred to R^3LD must be in either the A or B genome. In the A and B genomes, F_2 lines 4A, 3B and 5B gave segregation ratios of 3.6:1, 4.7:1 and 8.6:1 respectively. The other lines in the A and B genomes (except 3A which was largely sterile in F_1) either showed no segregation or very low frequencies of albinos. Therefore, one of chromosomes 3A, 4A, 3B or 5B might be the second involved in chlorophyll production.

TABLE 10.

SEGREGATION IN COMBINED F₂ LINES FROM 39 AND 40 CHROMOSOME
 F₁ PLANTS OF RESCUE MONOSOMICS X R³LD LINES
 WITH HIGH ALBINO FREQUENCIES

F ₂ Line	Number of Seedlings		Ratio
	Green	Albino	
R1A x R ³ LD	158	5	31.6:1
R2A x R ³ LD	115	0	
R3A x R ³ LD	2	0	
R4A x R ³ LD	-	-	
R5A x R ³ LD	193	13	14.8:1
R6A x R ³ LD	320	10	32 :1
R7A x R ³ LD	73	3	24.3:1
R1B x R ³ LD	185	0	
R2B x R ³ LD	43	0	
R3B x R ³ LD	14	3	4.7:1
R4B x R ³ LD	129	4	32.3:1
R5B x R ³ LD	-	-	
R6B x R ³ LD	104	0	
R7B x R ³ LD	190	15	12.7:1
R1D x R ³ LD	39	3	13 :1
R2D x R ³ LD	76	0	
R3D x R ³ LD	6	3	2 :1
R4D x R ³ LD	254	2	127 :1
R5D x R ³ LD	153	16	9.6 :1
R6D x R ³ LD	105	4	26.3 :1
R7D x R ³ LD	34	2	17 :1
Totals	2,193	83	

TABLE 11

SEGREGATION IN COMBINED F₂ LINES FROM 39 AND 40 CHROMOSOME
 F₁ PLANTS OF RESCUE MONOSOMICS X R³LD LINES
 WITH LOW ALBINO FREQUENCIES

F ₂ Line	Number of Seedlings		Ratio
	Green	Albino	
R1A x R ³ LD	29	1	29 : 1
R2A x R ³ LD	-	-	
R3A x R ³ LD	-	-	
R4A x R ³ LD	18	5	3.6 : 1
R5A x R ³ LD	107	0	
R6A x R ³ LD	65	1	65 : 1
R7A x R ³ LD	62	0	
R1B x R ³ LD	-	-	
R2B x R ³ LD	75	1	75 : 1
R3B x R ³ LD	-	-	
R4B x R ³ LD	139	3	46.3 : 1
R5B x R ³ LD	154	18	8.6 : 1
R6B x R ³ LD	68	0	
R7B x R ³ LD	87	0	
R1D x R ³ LD	-	-	
R2D x R ³ LD	247	6	41.2 : 1
R3D x R ³ LD	36	3	12 : 1
R4D x R ³ LD	103	4	25.8 : 1
R5D x R ³ LD	69	4	17.3 : 1
R6D x R ³ LD	230	6	38.3 : 1
R7D x R ³ LD	-	-	
Totals	1,489	52	

The nullisomic 3D plants were used as both female and male parents to cross with F₂ plants from double monosomics (4A, 3D) and (3B, 3D). No seeds were obtained however due to the sterility of nullisomic 3D.

V. F₂ LINES FROM 42 CHROMOSOME F₁ PLANTS

All 4298 F₂ seedlings were green. Most F₂ seedlings had 42 chromosomes but a few had 41 chromosomes.

VI. POLLEN TRANSMISSION RATE OF THE n-1 GAMETES

Transmission rates of the n-1 gametes through the male parents are included in Table 12. From male parents with high albino frequency, the pollen transmission rate of the n-1 gametes was 54.2% which is close to Bhowal's (1) observation of 61%. From male parents with low albino frequency, the pollen transmission rate of the n-1 gametes was 16.7%. If the transmission rates of the n-1 gametes through the female and male parents are 75% and 16.7% respectively, the frequency of F₁ plants with 42, 41 and 40 chromosomes should be 20.8%, 66.7% and 12.5% respectively which approaches the observed data shown in Tables 6 and 7. The samples in the high transmission rate are heterogeneous and in the cross of Rescue x R³LD 3-16-13 gave 5 disomic and 12 monosomic seedlings. This result contradicts the previously obtained data and due to the small population and the fact that a single cross is involved is necessarily disregarded.

TABLE 12.
POLLEN TRANSMISSION RATE OF THE $n-1$ GAMESSES

Cross	F ₁ Seedlings		Pollen transmission rate of the $n-1$ gametes
	Total	Chromosome number	
		42	41
<u>R²LD lines with high albino frequency</u>			
Rescue x R ² LD 3-16-11	7	6	1
Rescue x R ² LD 3-16-13	17	5	12
Totals	24	11	13
			54.2%
<u>R²LD lines with low albino frequency</u>			
Rescue x R ² LD 1-3-10	6	5	1
Rescue x R ² LD 1-6-13	24	20	4
Totals	30	25	5
			16.7%

VII MARQUIS X VERNAL CROSS

All 141 F_1 seedlings were green and had 35 chromosomes. Five F_1 plants were selfed. The remaining F_1 plants were backcrossed to Marquis. All F_2 and backcrossed F_1 seedlings were green. Twenty-three F_3 and 680 F_1 seedlings of backcrossed F_1 were also green. No albino seedlings was obtained from the progenies of Marquis x Vernal or Marquis² x Vernal. Smith and Harrington (16) used Vernal (C.I.3686). The Vernal emmer used in this experiment may be different.

GENERAL DISCUSSION AND CONCLUSIONS

It has been shown that the albinism in Lethal Durum is monogenic. In transferring the albinism to hexaploid wheat (R^3LD), the albino character is expressed only in the absence of chromosome 3D which would indicate that chromosome 3D of Rescue carries a gene for chlorophyll production. Sears (14,15) has also reported that chromosome 3D is involved in chlorophyll production. The gene transferred to R^3LD from Lethal Durum must be in either the A or B genome.

In plants nullisomic for chromosome 3D only the other locus or loci would be responsible for any segregation that occurred. Nine F_2 seedlings from a 40 chromosome F_1 plant of Rescue monosomic 3D x R^3LD consisted of 6 green and 3 albino seedlings. This result supports the assumption that there is only one other locus involved in chlorophyll production other than chromosome 3D. All green and albino F_2 seedlings from selfed nullisomic 3D should have 40 chromosomes. Actually one green seedling had 41 chromosomes and one albino had 39 chromosomes (shown in Plate IV, Figure 1). This may be due to asynapsis or desynapsis resulting in n and $n-2$ gametes instead of $n-1$ gametes (shown in Plate IV, Figure 2).

Due to the following reasons, a critical line in the A or B genome could not be positively identified from the segregation ratios of double monosomics.

- (1) Most 40 chromosome F_1 plants were very weak and highly sterile, especially homoeologous group III. This resulted in small F_2 populations.
- (2) When the double monosomics were selfed, the transmission frequency of each kind of gamete on both the female and male side was unknown. The expected frequencies of each genotypes therefore could not be calculated.
- (3) The frequency of nullisomic 3D plants might not be equal from line to line in which case the segregation for the A locus could not be compared.
- (4) Some seeds failed to germinate.

Sears (15) found that Neatby's virescent (v) is on 3B (III) of common wheat, v is antimorphic to V (or V_1) and that V has duplicates, V_2 and V_3 , on chromosomes 3A and 3D. If gene B and V_3 gene are at the same locus of chromosome 3D, they may be the same gene or alleles of a gene. Two genes, designated as A and B, involved in chlorophyll production have been assumed in this experiment. Because Triticum aestivum is a hexaploid species, it is reasonable to expect that a third chromosome also carries a gene for chlorophyll production. The fact that 3A and 3B are included in the possible group of critical chromosomes, it is likely that homoeologous group III is involved in this situation. It is possible that the same loci as Sears reported (14,15) may be involved.

Identification of the loci other than that in chromosome 3D is difficult due to lack of karyotype differences in the wheat chromosomes.

A possible means of identification would be to cross a plant of the constitution aaB- to Rescue monosomics 3A, 4A, 3B and 5B, the critical line should be of the genotype a-B- as compared to AaB- of non-critical lines. Large F₂ population and complete cytological examination might distinguish the critical line.

PLATE I

- Figure 1. Green and albino Lethal Durum seedlings.
- Figure 2. Nullisomic, monosomic and disomic F_1 hybrids of Rescue monosomic 3D x R^3LD .
- Figure 3. Green and albino F_2 seedlings of Rescue monosomics x R^3LD .

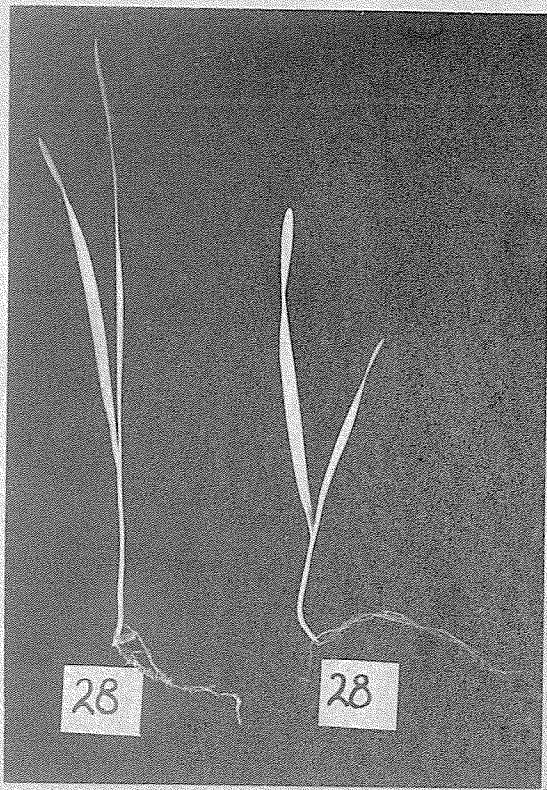


Figure 1



Figure 2

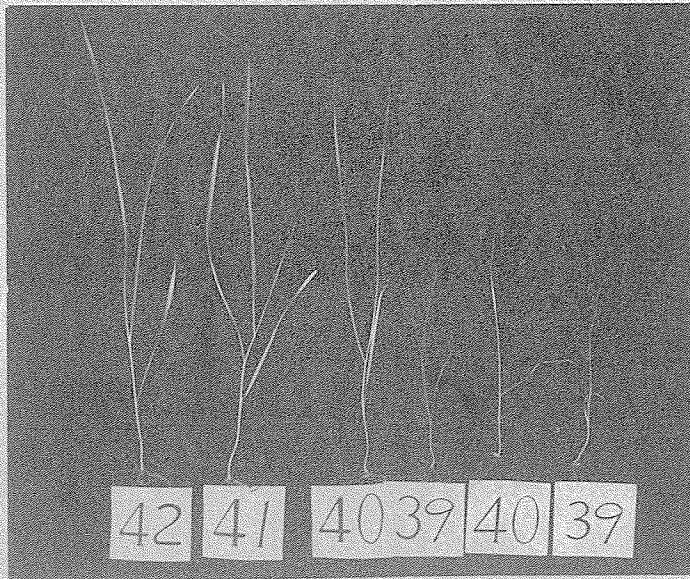


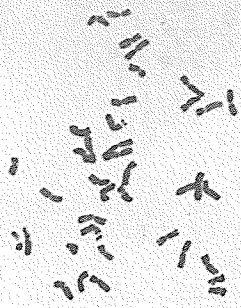
Figure 3

PLATE II

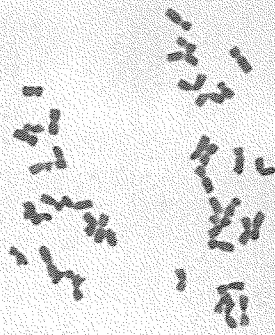
Mitotic metaphase configurations of
green and albino F₂ seedlings of
Rescue monosomics x R³LD.

Figures 1-2. 39 and 40 chromosome
albino seedlings.

Figures 3-6. 39, 40, 41 and 42
chromosome green seed-
lings.



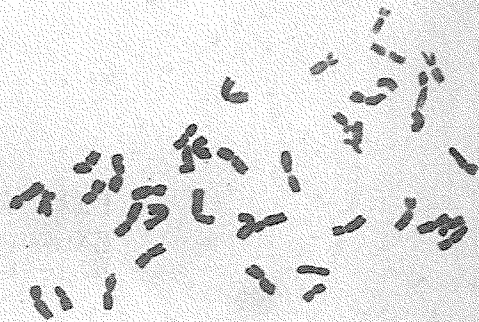
1



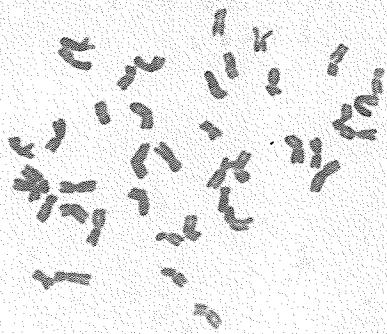
2



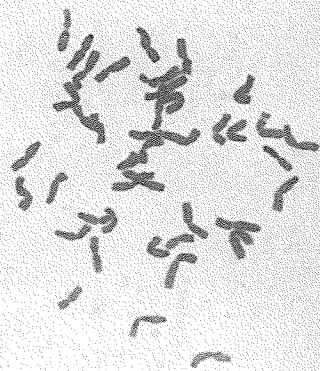
3



4



5



6

PLATE III

Meiotic configurations of double monosomic
and nullisomic F_1 Rescue monosomic x R^3LD
hybrids.

Figure 1. Anaphase of a double monosomic

Figure 2. Metaphase of nullisomic 3D with
20 bivalents.

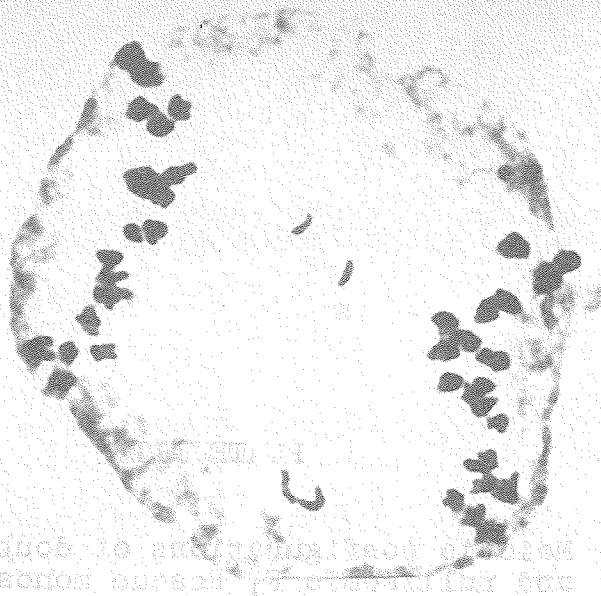


Figure 1

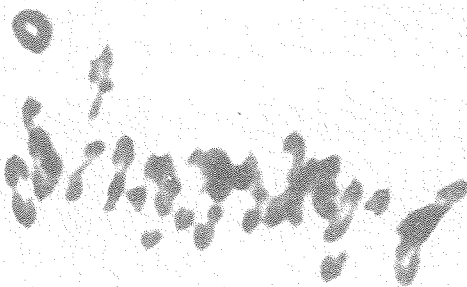


Figure 2

PLATE IV

Figure 1. Green and albino F_2 seedlings of Rescue monosomic $3D \times R^3LD$.

Figure 2. Anaphase I of meiosis of an F_1 double monosomic illustrating possible formation of $n-2$ gametes.

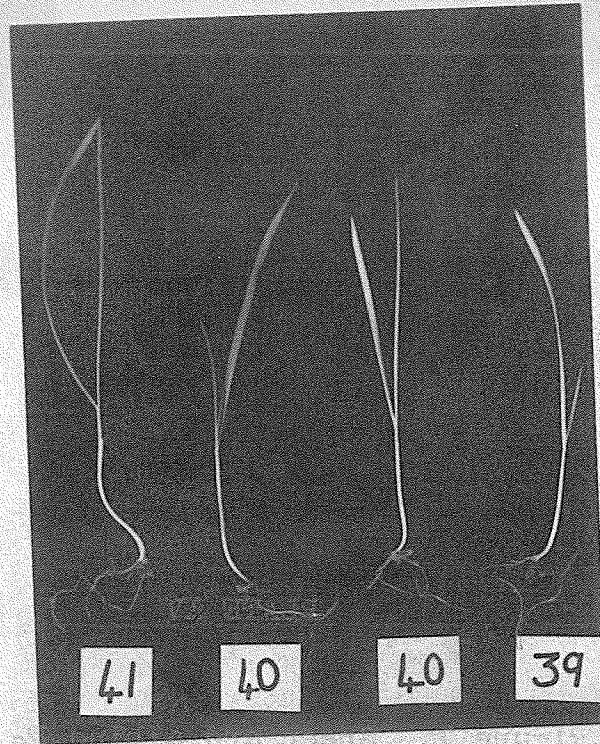


Figure 1

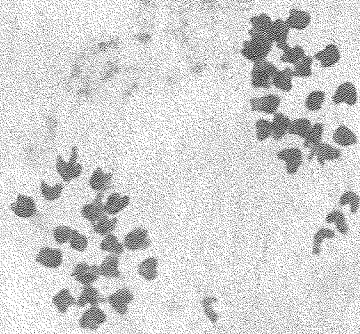


Figure 2

REFERENCES

1. Bhowal, J.G. An unusual transmission rate of the deficient male gamete in a substitution monosomic of chromosome 3D in wheat. *Can.J. Bot.* 42: 1321-1328, 1964.
2. Bhowal, J.G. Comparative growth and function of normal and deficient pollen in a substitution monosomic of chromosome 3D in wheat. *Can. J. Bot.* 42: 1329-1333, 1964.
3. Froier, K. Genetical studies on the chlorophyll apparatus in oats and wheat. *Hereditas* XXXII: 297-406, 1946.
4. Harrington, J. B. and W. K. Smith. Yellow seedlings in wheat. *Sci. Agric.* IX: 147-153, 1928.
5. Philp, J. Aberrant albinism in polyploid oats. *J. Genet.* XXX: 267-302, 1935.
6. Larson, R.I. Inheritance of the type of solid stem in Golden Ball (Triticum durum) II. Cytogenetics of the relation between solid stem and other morphological characters in hexaploid F₅ lines of a hybrid with rescue (T. aestivum). *Can. J. Bot.* 37: 1207-1216, 1959.
7. Larson, R.I. and H. J. Perkins. Photosynthesis in a line of wheat nullisomic for chromosome 3D (XVI). *Can. J. Genet. Cytol.* 3: 396-402, 1961.

8. McGinnis, R. C. and D. K. Taylor. The association of a gene for chlorophyll production with a specific chromosome in *Avena sativa*. *Can. J. Genet. Cytol.* 3: 436-443, 1961.
9. McGinnis, R. C. and G. Y. Andrews. The identification of a second chromosome involved in chlorophyll production in *Avena sativa*. *Can. J. Genet. Cytol.* 4: 1-5, 1962.
10. McGinnis, R. C. G. Y. Andrews and R. I. H. McKenzie. Determination of the chromosome arm carrying a gene for chlorophyll production in *Avena sativa*. *Can. J. Genet. Cytol.* 5: 57-59, 1963.
11. Neatby, K. W. A chlorophyll mutation in wheat. *J. Heredity* 24: 159-162, 1933.
12. Rajhathy, T. A standard karyotype for *Avena sativa*. *Can. J. Genet. Cytol.* 5: 127-132, 1963.
13. Sears, E. R. The aneuploids of common wheat. *Missouri Agr. Expt. Sta. Research Bull.* 572: 1-58, 1954.
14. Sears, E. R. Neatby's virescent, a chlorophyll aberration in common wheat. *Genetics* 44: 534, 1959.
15. Sears, E. R. Gene evolution in polyploid wheat. *Proc. XI. Int. Congr. Genet.* 1: 123-124, 1963.

16. Smith, W.K. and J.B. Harrington. Wheat albinos. J. Heredity 20: 19-20, 1929.
17. Stadler, L.J. Chromosome number and the mutation rate in Avena and Triticum. Proc. Nat. Acad. Sci. 15: 876-881, 1929.
18. Steinitz-Sears, L.M. Cytogenetic studies bearing on the nature of the centromere. Proc. XI Int. Congr. Genet. 1: 123, 1963.