A STUDY OF THE INHERITANCE OF GROWTH HABIT AND OTHER CHARACTERS IN COMMON WHEAT

by

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A Thesis
Submitted to the Committee on Graduate Studies
in Partial Fulfilment of the Degree of
Master of Science

The University of Manitoba
May 1956

ABSTRACT

In order to determine the mode of inheritance of growth habit, awn development and spike type in common wheat a conventional and a monosomic analysis was carried out on the F_2 generations from the crosses between the winter varieties, Kharkov and Elgin, and the spring variety, Chinese Spring.

The inheritance of growth habit appears to be governed by three main factor pairs one of which is located in chromosome XVIII of the varieties studied.

Awn inheritance appears to be controlled by a complex interaction of genes. In Chinese Spring, genes related to awn inheritance are located in chromosomes II, VII, VIII, and X. The awned condition is recessive to the awnless condition.

The short dense spike type of the compactum wheats is dominant to the lax headed vulgare types. The main genes governing spike type were found to be in chromosomes IX and XX of Chinese Spring. In addition, there appear to be several modifying genes in other chromosomes.

Use of the monosomic analysis technique is regarded as having value in determination of the mode of inheritance of qualitative characters but is of little use in studying the inheritance of quantitative characters.

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ACKNOWLEDGMENTS

The writer wishes to express sincere appreciation to Dr. B. C. Jenkins for his assistance and guidance throughout the course of this study, for his constructive criticisms and suggestions, for the improvement of the manuscript and for his aid in preparing the photographs appearing in this thesis.

Thanks is also extended to Professor L. H. Shebeski for reading the manuscript and for his many suggestions for its improvement and to Mr. H. R. Hikida for taking many of the photographs.

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

INTRODUCTION

Prior to the development of the complete series of monosomics and nullisomics in common wheat by Dr. Sears the scope of work on wheat genetics was limited to the determination of the number of genes affecting the expression of any specified character. In general, gene position could not be determined beyond a genomic location.

Following the establishment of the complete aneuploid series in Chinese Spring, a variety of common wheat, it became possible to locate specific genes in specific chromosomes. The use of the aneuploid series facilitates linkage group identification in addition to gene number calculation.

In the short time that the aneuploid series has been available to plant breeders and geneticists a great deal of controversy has developed regarding the value of the F_2 monosomic line analysis method as a means of determining the number of genes affecting the expression of a specific character. The reason for this is the lack of agreement between results obtained using this method and results obtained from conventional genetic studies.

The aim of this project was to determine the number and location of the genes affecting the expression of spring versus winter growth habit in three varieties of common wheat by means of the F_2 monosomic line analysis method and to compare the results with those obtained from a conventional analysis of a normal F_2 population. In addition the inheritance of awning and spike type have been noted and will be described in some detail.

This project has been carried out as a sub-project of a broader program aimed at increasing the hardiness of winter wheat by substituting rye chromosomes for certain chromosomes of the wheat complement. It is hoped that information gained from this study will be of fundamental value in obtaining this final result.

LITERATURE REVIEW

Interest in wheat genetics developed soon after the rediscovery of Mendel's laws and among the earliest characters studied were growth habit, awning and spike type.

Review of Growth Habit Studies

According to Cooper (6), Spillman in 1909 and Tschermak in 1910, reported that growth habit was monogenically inherited. Spillman reported spring habit to be dominant, whereas Tschermak found winter habit to be dominant. Since these early investigations many similar studies have been carried out and monogenic (6), digenic (2, 6, and 30), trigenic (23) and multigenic (2, 10, and 12) inheritance have been reported. In the majority of cases spring habit was reported to be dominant.

Cooper (6) using three winter varieties, Dawson's Golden Chaff, Kanred and Fulcaster, and two spring varieties, Marquis and Minnesota No. 169 made all possible crosses between the spring and winter varieties. In the F_2 of crosses between Marquis and the three winter varieties he obtained ratios of 13 spring plants to 3 winter habit plants. From crosses involving Minnesota No. 169 and the winter varieties he obtained F_2 ratios of 3 spring to 1 winter. It was concluded that two pairs of factors governed the expression of growth habit and that one of these pairs, when present in the dominant form, prevents the expression of winter habit. Cooper postulated the genotype of Marquis to be ssII, that of Minnesota No. 169 to be SSII and that of the winter varieties to be SSii. Although the dominant allele S for winter habit is present in Minnesota No. 169 its expression is prevented by the dominant inhibitor.

In the F_2 of a cross between Hybrid 128 and Velvet Node, Powers (23) found that three major factor pairs were interacting in the expression of growth habit. He postulated the factors for spring habit to be AA, BB and cc whereas the opposite alleles produced winter habit when all were present in the homozygous condition. Macindoe (20) found this hypothesis fitted the results obtained from the F_2 population from the cross of Charter x Winter Minflor. He also found, in a cross of Thatcher Selection x Winter Minflor, that growth habit was simply inherited.

Aamodt (2) classified 5253 F_2 plants of the cross Marquis x Kanred and found 980 plants as early as Marquis, 442 with complete winter habit and 3831 that occupied a complete intermediate range. He concluded that the inheritance of growth habit must be extremely complex. Gaines and Singleton (10) working with a cross of Marquis x Turkey drew a similar conclusion.

Limited investigation has been made as to the chromosomal location of growth habit genes. Unrau (32) has reported that duplicate genes condition growth habit in a cross between Chinese Spring and Hymar. He located one of these genes in chromosome IX. Sears (24) working with the Chinese Spring nullisomic series found lines II, V, VIII, IX, X, XVI and

XVIII all to be later in maturity than the normal diploid plants. Of these seven lines XVIII was extremely late. In studying the inheritance of winter injury resistance in hybrid lines from crosses of the Chinese Spring monosomes by Pawnee, Heyne and Livers (14) found monosomic XVIII lines very hardy and monosomic VI lines to be highly susceptible to winter injury.

Review of Awn Inheritance Studies

Awn inheritance like growth habit has been thoroughly studied and reports of monogenic (10, 30), digenic (30) and trigenic (33), inheritance have been made by various workers. The lack of agreement is probably due to varietal differences and to classification difficulties which occur when analysis is attempted. Watkins and Ellerton (33) have made a thorough review of awn inheritance and have postulated that in hexaploid wheats awn expression is governed by genes at three loci. These loci they described as the B_1 locus with alleles b_1 and b_{1a}, the B_2 locus with the allele b_2 and the Hd locus with the allele hd. The B_1 and B_2 genes in the dominant state are duplicate genes producing awnlessness and the recessive alleles b_1 and b_2 in the homozygous condition result in full awn production. The b_{1a} gene at the B_1 locus and possibly a similar gene at the B_2 locus produce half awns. The Hd gene is dominant for shortened and recurved, twisted awns and in the dominant homozygous state results in the so-called hooded type. From the 12 possible homozygous genotypes that can occur there are 6 distinct phenotypes which along with the numerous heterozygous possibilities explain the wide range of intermediates and the apparent continuous variation in the F_2 populations.

Sears (24) reports the Hd locus to be on chromosome VIII, the B_2 locus on chromosome X and the b_1 locus to be on chromosome IX of Chinese Spring. Unrau (32) has confirmed the above findings. Sears (24) has located awn promoting genes on chromosomes II and XX which have been shown to be recessive in Chinese Spring and have been designated as a_1 and a_2.

Heyne and Livers (14) have reported abnormal awn expression on monosomic lines VIII, IX, X, XII, XV, XVI, and XXI of hybrids between the Chinese Spring monosomes and awned Pawnee. In addition to the genes in chromosomes VIII and X located by Sears they have postulated the presence of three modifying genes on chromosomes XII, XVI, and XXI. They have designated these as the A_3, A_4, and A_5 series of alleles.

Summation of the above findings and postulations would ascribe to Chinese Spring the following genotype: Hd on VIII, b_1 on IX, B_2 on X, a_1 on II, a_2 on XX, A_3 on XII, A_4 on XVI, and A_5 on chromosome XXI. Heyne and Livers (14) postulated that Pawnee had the opposite alleles in all cases except for the A_1 and A_2 locus for which they had no proof.

Review of Spike Type Inheritance

Spike density has been shown by Spillman and Gaines (according to Hayes and Immer 13) to be governed by one main gene pair as concerns the difference between the lax head type of vulgare wheats and the compactum type head. When interspecific crosses are made between the vulgare and club wheats transgressive segregation usually occurs and head types more extreme than either parent are obtained.

Unrau (32) located the main gene for club head type on chromosome XX of the club variety Hymar. This gene has been designated as C and in the dominant state produces the compactum type head. Evidence obtained by Unrau shows that complete dominance is expressed in the heterozygous state.

MATERIALS AND METHODS

Before describing in detail the procedure followed in this program it is deemed necessary to outline briefly the general method followed in both the conventional and monosomic type of analysis.

In determining the inheritance of a specific character in the conventional way, two individuals expressing diverse phenotypes of the character in question are crossed, for example an awned and an awnless variety of wheat. The F_1 generation will be phenotypically uniform and will indicate which if either parental type is dominant. A relatively large F_2 population is grown and from it a genetic ratio of the segregating types is established. From this ratio a provisional hypothesis, regarding the mode of inheritance and the number of genes involved is derived. Using this hypothesis as a basis, a theoretical ratio is calculated and the theoretical and actual ratios are then compared by means of the chi square test. The P value is the probability of obtaining the actual ratio from a population segregating in accordance with the hypothesis. The final test of the hypothesis is obtained by growing the F_3 generation and determining by means of the chi square test whether the segregation ratio obtained agrees with the theoretical expectation. In polyploid species such as wheat, where identified linkage groups are lacking, gene location can not be determined by conventional means.

When the F_2 monosomic line analysis is used the usual procedure is to determine the number of genes involved by the conventional manner. The gene location is then determined by crossing one variety with the 21 monosomes or nullisomes of the other parental variety and carrying the progeny of each of the 21 crosses on to the F_2 generation and comparing the ratio obtained from each deficient line with the ratio obtained from the normal F_2 population.

The abnormal ratios produced by certain deficient lines are regarded as having resulted from the fact that the missing chromosome carries one or more factors directly or indirectly influencing the expression of the character in question. Simultaneous determination of gene number and location is possible by this method.

Three wheat varieties, Chinese Spring, Kharkov and Elgin, were utilized. The first two are varieties of common wheat Triticum aestivum ssp. vulgare (Vill. Host.) MacKey, the latter is a variety of Triticum aestivum ssp. compactum (Host.) MacKey, or club wheat. These three varieties are shown in plate I (figs. a, b and c).

Chinese Spring may be described as a moderately early maturing spring variety having a lax, awnless spike. This variety was used in reciprocal crosses with the two winter varieties and as the source of the 21 deficient aneuploid lines.

Kharkov is a hardy winter wheat characterized by a fully awned, lax spike. Kharkov was used as the male parent in the crosses with the 21 deficient lines and was reciprocally crossed with the other two varieties.

Elgin, a typical winter club wheat, has a very short, dense spike and is completely awnless. It was used in the same manner as was Kharkov.

In the spring of 1954 seed of the 21 Chinese Spring monosomic lines, normal Chinese Spring and vernalized seed of the winter varieties was sown at Saskatoon.

During the course of the growing season cytological identification of at least two monosomic plants in each of the deficient lines was determined by pollen mother cell observation. These plants served as the female parents in crosses with Kharkov and Elgin, resulting in 42 separate crosses. In addition reciprocal crosses were made between the three varieties, making a combined total of 48 crosses. Suitable seed set was obtained in all crosses except in the crosses between lines IX and XXI with Elgin and line XXI with Kharkov. These three crosses were successfully obtained in the greenhouse the following winter with the result that they were one generation behind the other 39 lines during the course of the study.

During the winter of 1954-1955 a maximum of six F_1 plants from each of the 39 deficient line crosses were grown to maturity in the greenhouse and seed was collected from all surviving plants. The majority of these F_1 plants were cytologically identified as to whether they were of normal or monosomic constitution. During the same period F_1 populations of the normal parent crosses were grown so as to obtain seed for the conventional F_2 analysis. In addition a small F_2 population (200 plants), from the cross Kharkov x Chinese Spring and its reciprocal, was grown in order to obtain an estimate of the number of genes involved in the inheritance of growth habit. Small representative stocks of each parent were grown for comparative purposes.

In the spring of 1955 seed from all above mentioned F_1 plants was sown in the field. This resulted in a maximum of six F_2 lines representing each of the deficient line crosses. The normal F_2 population was divided in half and sown at two dates two weeks apart. In addition all available F_1 reserve seed and seed of each of the parents was sown for comparative purposes. In cases where the F_1 plants from the deficient line crosses had not been checked for chromosomal constitution a random sample of four plants was taken from the F_2 line and these plants were checked for chromosome number. If a monosomic plant was found within a sample the F_1 parent was regarded as having been a monosomic, if all four plants were found to be normal the F_1 parent was assumed to have been normal.

With regard to the genetic analyses, the F_2 populations with Kharkov parentage were analysed for growth habit and awn inheritance. The F_2 populations with Elgin parentage were analysed for the above listed characters and in addition were analysed for spike density inheritance.

The analysis of the F_2 populations for growth habit inheritance consisted of sorting the plants in each of the populations into three distinct growth habit groups namely, early spring, intermediate and winter. The early spring class was characterized by plants that headed as early as the Chinese Spring parent. Plants expressing complete vegetative growth similar to the winter parents were classed as winter and all other plants were classed as intermediate. Ratios from the normal F_2 populations were used as the bases on which provisional genetic hypotheses were established. Theoretical ratios based on the hypotheses were calculated and the actual and theoretical ratios were compared by means of the chi square test. The ratios obtained from the deficient F_2 lines were compared to the ratios obtained from the normal F_2 populations in order to determine which of the deficiencies had caused disturbances in the segregation ratios.

The analyses for awn inheritance consisted of sorting the headed plants in the F_2 populations into five awn expression groups namely, awnless, tip awned, intermediate, half awned and fully awned. The procedure of setting up provisional hypotheses and determining which deficiencies caused ratio disturbances was similar to that used in relation to growth habit inheritance.

The F_2 populations with Elgin parentage were analysed for spike type inheritance. This was done by classifying the headed plants in each population as either club headed, semi-club, intermediate, semi- lax, or lax. The analytical procedure to determine the mode of inheritance was as outlined for the other characters.

Portions of the normal F_2 populations from the reciprocal crosses between Chinese Spring and Kharkov were sown at three different dates, October 31, 1954; May 10, 1955 and May 25, 1955. The entire population from the crosses between Chinese Spring and Elgin and all the deficient F_2 lines were sown at the second date listed above. The analyses of each of the populations was commenced at the time of maturation of Chinese Spring sown at the same date.

RESULTS AND DISCUSSION

Growth Habit Inheritance

(a) Conventional Analyses of the Normal Populations

The F_1 generation from the reciprocal crosses between Chinese Spring and Kharkov was identical in all observable traits, spring growth habit was completely dominant and the plants were further characterized by lax spikes and moderately long tip awns. Plate I (fig. d) shows a typical F_1 spike.

The F_1 generation from the crosses between Chinese Spring and Elgin expressed complete spring habit and was characterized by plants with very short, dense, awnless spikes. Plate I (fig. e) shows a typical F_1 spike.

The F_1 generation from the reciprocal crosses between the winter varieties expressed complete winter habit. These lines were not carried beyond the F_1 generation so evidence is not available to prove that segregation for growth habit would not occur in the next generation.

Results from the classification of the F_2 populations from the reciprocal crosses between Chinese Spring and Kharkov are contained in Table I.

TABLE I Growth Habit Data from the Analysis of the F_2 Generation from the Reciprocal Crosses Between Chinese Spring and Kharkov.

		Growth Habit Expressed		
Date	Cross	Early Spring	Intermediate	Winter
I	Ch. Sp. x Khar.	56	34	10
	Khar. x Ch. Sp.	55	33	12
	Date Total	111	67	22
II	Ch. Sp. x Khar.	363	335	510
	Khar. x Ch. Sp.	168	133	215
	Date Total	531	468	725
III	Ch. Sp. x Khar.	72	65	206
	Khar. x Ch. Sp.	128	142	330
	Date Total	200	207	536

The ratios obtained reveal that date of seeding has a strong influence on the expression of growth habit. The later seeding dates resulted in a larger proportions of the population expressing winter habit. Such a result may be due to seasonal changes as regards day length and temperature and may be indicative of a genic threshold phenomenon wherein only plants with a genotype having spring habit genes at the majority of the growth habit influencing loci are capable of heading when sown late in the season. The proportion of spring habit to winter habit genes required to induce heading must therefore be dependant on the environment.

An explanation of the complex ratios obtained at each of the seeding dates can be made by means of the hypothesis expounded by Powers (23) wherein three main factor pairs AA, BB and CC govern growth habit. The assumption is made that the genotype AABBcc is the earliest spring type and that the genotype aabbCC is the latest winter type and that all other genotypes combine to form the complete intermediate range. The genes are presumed to act in a cumulative manner but may be of varying strengths.

The results of the monosomic analysis indicated that Chinese Spring, although a typical spring variety, carries factors for winter growth habit consequently it is postulated that the genotype of Chinese Spring is AABBCC whereas that of the winter varieties is aabbCC (a difference of two main factor pairs). The crosses would therefore result in F_1 plants with the genotype AaBbCC and nine F_2 genotypes in the ratio of 1 AABBCC:2 AaBBCC:2 AABbCC:4 AaBbCC:1 AAbbCC:2 AabbCC:1 aaBBCC:2 aaBbCC:1 aabbCC.

The date I ratio of 111 early spring:67 intermediate: 22 winter can be reclassified as 111:89 which fits a 9:7 ratio with a chi square value of .046 or a P value above .50. This would indicate that all genotypes homozygous or heterozygous for the genes A and B are capable of inducing heading as early as it occurs in Chinese Spring. This also indicates that a certain interaction exists between A and B in that the genotype AaBbCC has stronger spring habit producing tendencies than AAbbCC or aaBBCC.

The date II ratio of 531 early spring:468 intermediate:725 winter fits a 5:4:7 ratio with a chi square value of 4.17 and a corresponding P value between 0.10 and 0.20. Such a ratio is explained by assuming that the genotypes AABBCC, AaBBCC and AABbCC produce early spring plants, the genotype AaBbCC the intermediate expression and that all other genotypes result in winter habit.

The ratio of 200 early spring:207 intermediate:536 winter obtained from the third date of seeding fits a 3:13 ratio when the intermediate and winter classes are grouped. The chi square value for such a fit is 3.75 which gives a P value above 0.05. It is assumed that only the genotype AABBCC and either AaBBCC or AABbCC are able to induce heading of plants sown at the latest date. If such a hypothesis is correct it indicates that the genes A and B are not of equal strength.

The F_2 population from the cross of Chinese Spring and Elgin produced a ratio of 251 early spring:160 intermediate:390 winter. This ratio fails to fit a 5:4:7 ratio but fits a 5:11 ratio when the intermediate and winter classes are grouped with a chi square value of .003 and a P value above 0.95. The hypothesis used to explain the result from the second date of the Chinese Spring-Kharkov population will likewise explain the 5:11 ratio if it is assumed that some of the plants with the genotype AaBbCC have been misclassified.

Support for the above postulation is gained from the fact that the F_1 plants from the first date were classed as early spring, those from the second date as intermediate and plants from the third date were borderline between intermediate and winter. This classification agrees with the above postulated classification of the plants with the genotype AaBbCC which is assumed to be the F_1 genotype.

Results from the normal F_2 analysis leads to the conclusion that only two main factor differences, influencing growth habit, exist between Chinese Spring and the two winter varieties.

(b) Monosomic Analysis of the Deficient Populations

The deficient F_1 lines from the crosses between the Chinese Spring monosomes and Kharkov show little variation from the normal F_1 spike as can be seen when the twenty (monosomics I to XX) typical monosomic F_1 spikes in plate II (figs. a to t inclusive) are compared to the normal F_1 spike shown in plate I (fig. d). Lines lacking chromosome II, V, VIII, IX, XIII, XVIII, or XXI were later maturing than the normal F_1 lines.

The deficient F_2 lines for each of the monosomes were classified in the same way as the normal F_2 lines and the ratios from each of the deficient lines were compared to the normal ratios for date II as previously described. The ratios and the chi square and P values for each of the Chinese Spring monosomes x Kharkov F_2 lines are contained in Table II.

TABLE II Growth Habit Data from the Analysis of the Deficient F_2 Populations from the Crosses Between the Chinese Spring Monosomes and Kharkov.

F_2 Population	Growth Habit Expressed Early Spring	Intermediate	Winter	X^2	P
Normal	531	468	725		
Mono I	59	54	69	1.35	.5-.7
Mono II	12	7	15	1.13	.5-.7
Mono III	60	38	69	2.70	.3-.5
Mono IV	125	85	92	33.51	below .001
Mono V	38	16	25	11.76	below .01
Mono VI	66	53	67	3.01	.3-.5
Mono VII	96	33	72	34.30	below .001
Mono VIII	73	61	100	5.04	.1-.2
Mono IX	69	60	104	.69	.5-.7
Mono X	71	17	36	38.38	below .001
Mono XI	14	12	20	.61	.5-.7
Mono XII	129	55	84	31.04	below .001
Mono XIII	56	45	40	15.46	below .001
Mono XIV	78	33	49	20.47	below .001
Mono XV	110	55	91	17.00	below .001
Mono XVI	166	68	131	33.63	below .001
Mono XVII	146	28	51	110.11	below .001
Mono XVIII	0	0	250	----	below .001
Mono XIX	166	27	85	664.20	below .001
Mono XX	77	22	71	21.05	below .001

The analyses of the deficient F_2 lines from the Chinese Spring monosomes by Kharkov crosses revealed that 13 of the 20 deficient F_2 lines studied produced disturbed ratios indicating that possibly 13 chromosomes carry genes related to the inheritance of growth habit. Study of the ratios from the lines showing significant variations, reveals that 12 of the populations produced more early spring types than expected. Lines V and XIII are included in the above mentioned 12 lines but are on the borderline of significance and are regarded as non-carriers of growth habit genes. Line XVIII is unique in that all F_2 plants deficient for chromosome XVIII of Chinese Spring express complete winter habit. In addition, to lines IV, VII, X, XII, XIV, XV, XVI, XVII, XVIII, XIX and XX, it is assumed that chromosome XXI may carry a factor for growth habit due to the expression of delayed maturity in the F_1 generation. The final result appears to be that a maximum of 12 chromosomes in the F_1 generation from the cross of Chinese Spring x Kharkov may carry factors influencing the expression of growth habit.

The deficient F_1 lines from the crosses of the Chinese Spring monosomes by Elgin as shown in plate III (figs. a to s inclusive) were very similar in appearance to the normal F_1 spikes (plate I fig. b). All the deficient lines expressed spring habit and of the 19 studied only lines IX and XVIII were noticeably later than the normal F_1 lines.

From the F_2 data in Table III it appears that six chromosomes in the F_1 hybrid from the cross between Chinese Spring and Elgin carry factors related to the inheritance of growth habit. The lines involved are X, XII, XIV, XVIII, XIX and XX. Lines X, XII, XIV and XIX produce more spring types than expected and the other two lines produce an excess of winter habit plants (all plants deficient for chromosome XVIII of Chinese Spring are winter habit). It will be noted that the six lines involved in the Chinese Spring x Elgin cross are the same as six of those included in the 12 lines that produce disturbed ratios in the crosses between the Chinese Spring monosomes and Kharkov.

A comparison of the results from the conventional and from the monosomic line analyses shows little similarity. In attempting to relate the two results several possible explanations appear possible.

A first hypothesis is that three main factor pairs are involved in the inheritance of growth habit and that these three factors are influenced by a complex arrangement of modifying genes. From the data obtained it appears that the three main factor pairs may be located on chromosomes XVIII, XIX and XX. Chromosome XVIII carries a strong gene for winter habit in the winter varieties and a correspondingly strong spring habit allele in Chinese Spring. Chromosome XIX is believed to carry a gene for winter habit

TABLE III Growth Habit Data from the Analysis of the Deficient F_2 Populations from the Crosses Between the Chinese Spring Monosomes and Kharkov.

	Growth Habit Expressed				
F_2 Population	Early Spring	Inter-mediate	Winter	X^2	P
Normal	273	179	436		
Mono I	67	42	109	.89	.5-.7
Mono II	32	12	44	3.59	.3-.5
Mono III	68	42	129	2.56	.3-.5
Mono IV	113	62	136	5.88	.1-.2
Mono V	42	37	91	3.07	.3-.5
Mono VI	63	43	99	.64	.5-.7
Mono VII	28	14	61	4.88	.1-.2
Mono VIII	12	3	20	4.05	.2-.3
Mono IX	-*	-	-	-	-
Mono X	62	24	45	30.10	below .001
Mono XI	44	31	55	3.36	.3-.5
Mono XII	97	18	100	31.20	below .001
Mono XIII	17	16	52	13.16	below .01
Mono XIV	71	15	50	30.73	below .001
Mono XV	8	12	23	7.74	.1-.2
Mono XVI	-*	-	-	-	-
Mono XVII	44	31	55	3.36	.3-.5
Mono XVIII	-*	-	-	-	-
Mono XIX	83	46	77	19.19	below .001
Mono XX	42	32	142	24.15	below .001

* No available data due to small size of the population.

in Chinese Spring as well as in the winter varieties. Chromosome XX like XVIII is thought to carry a spring habit allele in Chinese Spring and a winter habit allele in the winter varieties. The following facts are the bases on which the foregoing conclusions have been made.

1. All F_2 plants deficient for chromosome XVIII of Chinese Spring express winter growth habit.
2. F_2 lines deficient for chromosome XIX of Chinese Spring contain more spring habit plants than theoretically expected.
3. F_2 lines deficient for chromosome XX of Chinese Spring contain a higher proportion of winter habit plants than expected.

If the above conclusions are correct it is necessary to assume that nine chromosomes in the F_1 of Chinese Spring x Kharkov carry modifying genes and that three chromosomes in the F_1 of Chinese Spring x Elgin carry factors modifying growth habit. From Tables II and III it would appear that the majority of these modifiers tend to delay plant maturity.

A second hypothesis is that the genes in hexaploid wheat act in complementary groups so that three genes act as a solitary unit and all three members of a group must be present in order for the unit to express itself. According to such a hypothesis there would be four units controlling growth habit in Kharkov and only two units involved in Chinese Spring and Elgin. Although this hypothesis is not rejected it is felt that insufficient information is available to warrant further discussion.

A third possible explanation is that the disturbed ratios are caused by a physiological unbalance due to the removal of a chromosome and that the missing chromosome may not carry any factors related directly to the inheritance of growth habit.

A fourth and very probable explanation is that the use of a normal F_2 population ratio as the basis for determining which deficiencies cause ratio disturbances is invalid. The reason for this lack of validity is the fact that each of the deficient lines reacts differently to the environment due to the physiological unbalance; this results in the fact that the physiological age of the deficient lines differ, resulting in the fact that each line is confronted with a different physiological age-environment relationship. The result is that the physiological and genetical factors are interacting to produce the ratios and the factors are inseparable. This means that the normal F_2 population and the individual deficient lines may not have developed at the same rate and have therefore developed under different environmental conditions even though the plants are of the same chronological age.

The opinion of the author is that there are two main factor differences between the winter varieties and Chinese Spring. This conclusion is based entirely on the results from the conventional analysis. The results from the monosomic line analysis have led to the conclusion that one of the main factors for growth habit is located on chromosome XVIII of Chinese Spring. The remainder of the data derived from the monosomic analysis of growth habit is regarded as having limited validity due to the following reasons.

1. The removal of a complete chromosome causes a severe physiological unbalance in the plant which tends to mask the effect of the removal of the genic material.
2. The fact that the environment has such a strong influence on the expression of growth habit invalidates the use of a normal F_2 population as the basis with which the deficient F_2 lines are compared. The maturity date of the monosomics is influenced by the physiological as well as the genetic factors and the two are inseparable.

The process of growing the F_3 generation in order to check the above hypotheses will be carried out during the coming growing season.

Awn Inheritance

(a) Conventional Analysis of the Normal Populations

The tip awned F_1 spikes from the reciprocal crosses between Chinese Spring and Kharkov, exemplified in plate I (fig. d), produced an F_2 generation containing a complete range of awn expression types from awnless to fully awned. The ratios obtained from the F_2 populations are contained in Table IV. Only the portions of the populations sown at the second and third dates were classified. A chi square value of 6.713 and a P value above 0.10 from a chi square test of heterogeniety showed that the date II ratios and the Kharkov x Chinese Spring ratio from the third date could be summated.

TABLE IV Awn Inheritance Data from the Analysis of the F_2 Generation from the Reciprocal Crosses Between Chinese Spring and Kharkov.

		Awn Expression*				
Date	Cross	Awn-less	Tip Awned	Inter-mediate	Half Awned	Fully Awned
II	Ch.Sp. x Khar.	162	157	94	72	25
	Khar. x Ch.Sp.	75	61	56	31	7
III	Ch.Sp. x Khar.	20	36	18	20	9
	Khar. x Ch.Sp.	55	53	25	26	9
	Grand Total**	292	271	175	139	41

* Plate IV (figs. a to e inclusive show typical spikes of each of the segregation classes.

** Chinese Spring x Kharkov ratio is not included.

The ratios obtained appear complex in the form in which they are presented but reclassification of the summated ratio into the form of 292 awnless to 626 plants with gradations of awning results in a ratio that will fit a ratio of 81:175 with a chi square value of .015 and a corresponding P value above 0.90. This indicates that a four factor hypothesis is tenable. If such a hypothesis were correct all plants with four dominant genes would be awnless and all other plants would express a degree of awning, in such a case the F_1 plants should be awnless as was not the case. The results obtained would indicate that the inheritance of awns is complex and can not be determined from the F_2 ratios available.

The F_1 generation from the cross of Chinese Spring x Elgin was awnless (plate I fig. d) and the F_2 generation contained a complete range of awn types in the ratio of 192 awnless:104 tip awned:25 intermediate:17 half awned:9 fully awned. The production of an awnless F_1 generation from the cross of two awnless varieties and the subsequent occurrence of awned plants in the F_2 generation must indicate that the production of awns depends on the cumulative action of certain genes. The above listed F_2 ratio fits a 9:7 ratio with a chi square value of .119 and a P value above 0.50 when reclassified as 192 awnless to 155 with gradations awning. Such a ratio is ordinarily regarded as resulting from the complementary action of dominant genes but such a hypothesis will not explain the production of an awnless F_1 generation from two awnless parents and the subsequent production of awned plants in the F_2 generation.

The conclusion drawn from the conventional analysis is that several factors interact in a complex manner to control awn inheritance and that the number and their mode of action cannot be satisfactorily postulated from the F_2 data without substantiation from F_3 segregation ratios.

(b) Monosomic Analysis of the Deficient Lines

Of the 20 deficient lines from the crosses between the Chinese Spring monosomes and Kharkov only lines II, VII, VIII, and X were distinguishable from the normal F_1 plants as regards awn expression. Of the exceptional lines II was completely awnless, VII was strongly tip awned and lines VIII and X were as heavily awned as the Kharkov parent.

The results from the analysis of the deficient F_2 lines are contained in Table V. They reveal that chromosomes II, VII, VIII, IX, X, and XVI may be involved in awn inheritance. This agrees with the expectations derived from the phenotypes of the F_1 generations except in the cases of lines IX and XVI which showed no abnormal variation in the F_1 generations.

TABLE V Awn Inheritance Data from the Analysis of the Deficient F_2 Populations from the Crosses Between the Chinese Spring Monosomes and Kharkov.

	Awn Expression						
F_2 Population	Awnless	Tip Awned	Intermediate	Half Awned	Fully Awned	X^2	P
Normal	292	271	175	139	41		
Mono I	24	26	15	13	5	.41	.95-.99
Mono II	10	3	2	1	0	7.86	.01-.05
Mono III	21	18	20	11	6	5.07	.2-.5
Mono IV	65	58	28	22	6	4.73	.3-.5
Mono V	17	14	6	7	3	1.61	.5-.7
Mono VI	36	25	14	11	4	3.69	.3-.5
Mono VII	13	38	44	17	7	35.59	below .001
Mono VIII	0	26	35	30	18	66.50	below .001
Mono IX	21	37	24	11	2	8.75	.01-.05
Mono X	0	19	22	28	10	44.32	below .001
Mono XI	6	9	2	1	0	4.02	.3-.5
Mono XII	49	46	31	23	9	.32	.95-.99
Mono XIII	33	21	16	17	6	3.89	.3-.5
Mono XIV	34	29	15	11	7	3.53	.3-.5
Mono XV	51	44	22	17	8	1.12	.5-.7
Mono XVI	72	73	32	23	5	8.69	.01-.05
Mono XVII	55	55	27	22	4	3.81	.3-.5
Mono XVIII*							
Mono XIX	64	58	34	18	8	4.25	.3-.5
Mono XX	30	22	20	15	2	3.08	.5-.7

* All Mono XVIII plants were winter habit.

Among the deficient F_1 lines from the crosses between the Chinese Spring monosomes and Elgin only lines II, VII and X differed from the normal F_1 plants. Line II was totally bald and the other two lines were slightly tip awned.

The results from the deficient F_2 analysis of the populations from the crosses between the Chinese Spring monosomes and Elgin are contained in Table VI. Lines lacking chromosomes II, VII and X of Chinese Spring produced disturbed ratios. The appearance of the F_1 plants deficient for chromosome VIII of Chinese Spring has led to the conclusion that a gene suppressing awn production is located on that chromosome.

The results from the monosomic analyses indicates that there are at least four factors involved in the inheritance of awns. In Chinese Spring these factors appear to be on chromosomes II, VII, VIII and X. Chromosome II appears to carry a gene weakly promoting awn development and the other three appear to carry factors suppressing awn development.

The conclusion drawn from the results of the monosomic analysis is that a minimum of four factors interact in a complex manner to control awn inheritance and that the complementary interaction of these so-called awn promoting and awn suppressing genes is too complex to be explained by the available data.

TABLE VI Awn Inheritance Data From the Analysis of the Deficient F_2 Populations from the Crosses Between the Chinese Spring Monosomes and Elgin.

F_2 Population	Awn Expression Awnless	Tip Awned	Intermediate	Half Awned	Fully Awned	X^2	P
Normal	210	114	26	18	11		
Mono I	36	13	11	3	2	8.76	.05-.1
Mono II	28	3	6	2	2	13.17	below .01
Mono III	38	27	7	4	1	2.43	.5-.7
Mono IV	86	44	8	7	1	3.20	.5-.7
Mono V	30	15	5	3	3	1.83	.5-.7
Mono VI	54	11	5	4	1	10.75	.01-.05
Mono VII	12	19	3	0	3	14.46	below .01
Mono VIII	3	7	1	1	1	6.36	.1-.2
Mono IX	-*	-	-	-	-	-	-
Mono X	18	23	17	6	8	60.29	below .001
Mono XI	31	20	3	3	1	.95	.5-.7
Mono XII	63	26	8	5	0	4.56	.3-.5
Mono XIII	32	14	8	1	2	6.06	.1-.2
Mono XIV	52	25	3	2	0	5.47	.2-.3
Mono XV	12	4	0	1	0	2.77	.5-.7
Mono XVI	-*	-	-	-	-	-	-
Mono XVII	24	4	5	1	1	8.29	.05-.1
Mono XVIII	-*	-	-	-	-	-	-
Mono XIX	67	28	6	7	2	2.74	.5-.7
Mono XX	25	24	6	4	2	5.27	.2-.3

* No available data due to the small size of the spring portion of the populations.

Spike Type Inheritance

(a) Conventional Analysis of the Normal Populations

The F_1 generation from the cross of Chinese Spring x Elgin was characterized by short, dense heads very like those of the Elgin parent. This indicates that the compactum head type is completely dominant to the head type of Chinese Spring.

Classification of the F_2 generation produced a ratio of 189 club:52 semi-club:25 intermediate:25 semi-lax:66 lax. The hypothesis tested is that there are two genes involved, one being the gene C which is dominant to c and produces the club type head and the other the S gene for speltoidy gene which is dominant to s, both of which are hypostatic to C. The assumed genotypes are CCSS for Elgin and ccss for Chinese Spring. The resulting F_1 generation from such a cross would have the genotype CcSs and would be club headed. The F_2 generation would segregate in a ratio of 12 C---:3 ccS-:1 ccss or 12 club:3 lax: 1 semi-lax. Reclassification of the F_2 ratio into the form of 266 dense types:66 lax:25 semi-lax produces a ratio that fits a 12:3:1 ratio with a chi square value of .314 and a corresponding P value of above 0.50.

(b) Monosomic Analysis of the Deficient Lines

The data from the classification of the deficient F_2 lines is contained in Table VII. From this data it appears that chromosomes XI, XVII, XIX and XX carry genes related

TABLE VII Spike Type Inheritance Data from the Analysis of the Deficient F_2 Populations from the Crosses Between the Chinese Spring Monosomes and Elgin.

	Head Type Expressed						
F_2 Population	Club	Semi-Club	Inter-mediate	Semi-lax	lax	X^2	P
Normal	190	52	25	27	66		
Mono I	31	16	11	8	13	9.18	.05-.1
Mono II	21	8	3	4	5	1.35	.5-.7
Mono III	37	15	7	7	11	1.78	.5-.7
Mono IV	77	27	18	12	22	6.97	.1-.2
Mono V	25	12	6	4	9	2.61	.5-.7
Mono VI	40	14	5	7	8	2.70	.5-.7
Mono VII	16	7	4	2	8	1.87	.5-.7
Mono VIII	8	3	1	0	1	2.07	.5-.7
Mono IX	-*	-	-	-	-	-	-
Mono X	40	8	4	10	10	7.57	.1-.2
Mono XI	16	15	4	13	14	24.92	below .001
Mono XII	54	16	5	12	15	4.51	.3-.5
Mono XIII	14	16	5	12	15	4.51	.3-.5
Mono XIV	30	19	5	8	20	6.94	.1-.2
Mono XV	7	4	2	3	1	4.94	.2-.3
Mono XVI	-*	-	-	-	-	-	-
Mono XVII	15	16	7	3	19	18.47	below .001
Mono XVIII	-*	-	-	-	-	-	-
Mono XIX	38	30	9	3	30	18.77	below .001
Mono XX	49	5	3	3	2	20.94	below .001

* No available data due to the small size of the spring portion of the population.

to spike type inheritance. In addition there is assumed to be a gene for speltoidy on chromosome IX of Chinese Spring as indicated by the appearance of F_1 plants monosomic for chromosome IX. The deficiency of chromosome XX increases the number of dense headed plants beyond expectations whereas the removal of any of the other four increases the proportion of lax types.

The genes C and S have previously been reported by Sears (29) and Unrau (32) to be on chromosomes IX and XX respectively. The factors that appear to be on chromosomes XI, XVII and XIX may have modifying effects.

GENERAL CONCLUSIONS AND SUMMARY

Growth Habit Inheritance

1. There is no distinct demarcation between spring and winter growth habit, instead there is a complete range of intermediates from early spring wheats to late winter wheats.
2. The expression of growth habit is strongly influenced by environmental conditions. Seeding a segregating F_2 population at different dates revealed that the proportion of spring habit plants in the population decreased with the later seeding dates. Such a phenomenon may indicate that a gene threshold level exists wherein the balance of spring to winter habit alleles required to induce heading increases for late sown plants.
3. Three main factor pairs are believed to govern growth habit in common wheat. The F_2 segregation ratios obtained from the normal F_2 populations lead to the conclusion that Chinese Spring and the two winter varieties, Kharkov and Elgin, differ in 2 pairs of these alleles and have one pair of winter habit producing alleles in common.
4. The three loci involved may be on chromosomes XVIII, XIX and XX. Of these three chromosomes only chromosome XVIII is a definite carrier of a growth habit factor.

Cooper (6), Powers (23) and MacIndoe (20) have reported two and three factor differences between varieties as regards the inheritance of growth habit. Results from this project would agree with their results.

Sears (29) and Unrau (32) have reported that chromosome IX of Chinese Spring carried a factor for spring habit of growth and Sears (24) has reported that lines deficient for chromosome XVIII of Chinese Spring were very late. Findings from this experiment agree that chromosome XVIII is involved but does not support the report that a growth habit factor is located on chromosome IX of Chinese Spring.

Awn Inheritance

1. Awn inheritance appears to be governed by a complex interaction of several genes.
2. There.are at least four factors involved in the inheritance of awns. These factors are located on chromosomes II, VII, VIII, and X of the variety Chinese Spring. The winter varieties probably carry opposite alleles on these four chromosomes. Other factors may be involved which were not detected due to the small size of some of the deficient populations.
3. The production of complete awning must be due to transgressive segregation or complementary action of recessive genes as evidenced by the fact that a small number of fully awned individuals occur in the F_2 generation from the cross between the two awnless varieties, Chinese Spring and Elgin.

The occurrence of genes related to awn inheritance on chromosomes II, VIII, IX, and X of Chinese Spring have been reported by Sears (29) and Unrau (32). The present findings agree except in the case of chromosome IX which does not appear to carry the awn suppressor reported by the above investigators. In the present study chromosome VII appears to carry such a suppressor, this may indicate that there has been a translocation between chromosomes VII and IX in the Chinese Spring stock used in this study.

Spike Type Inheritance

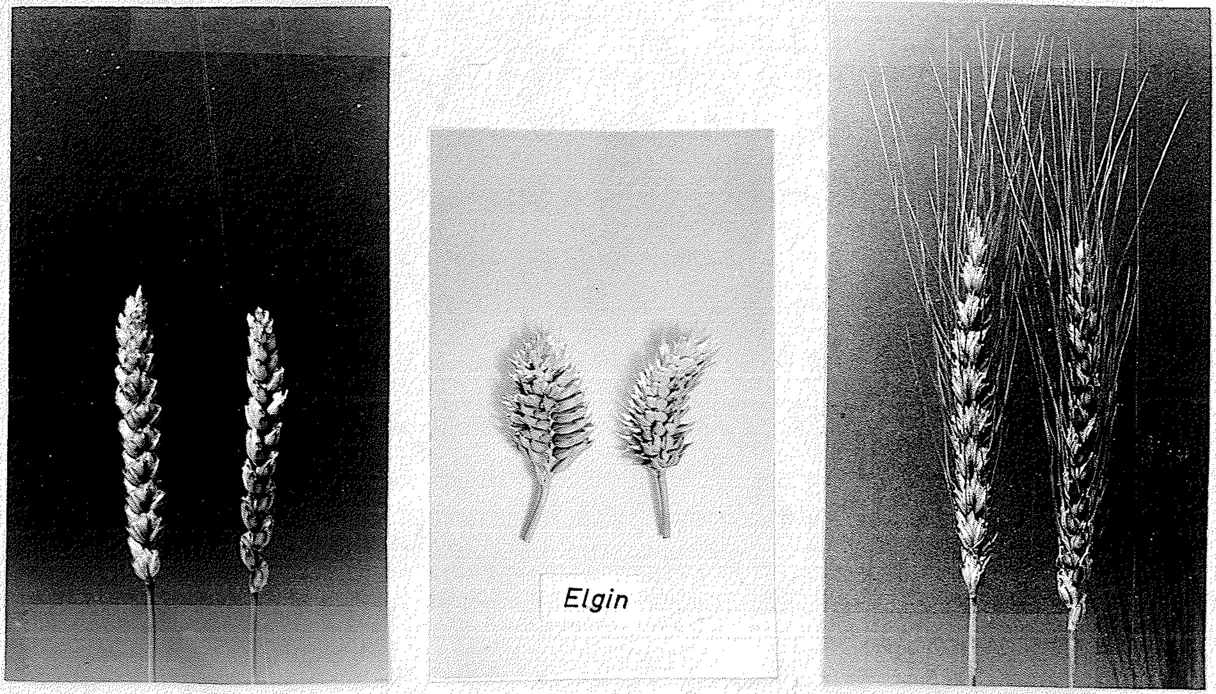
1. The short dense spike type of Elgin is completely dominant to the lax head type of Chinese Spring.
2. The main factors controlling spike type are located on chromosomes IX and XX of Chinese Spring. Chromosome IX carries a factor for increased density and chromosome XX carries a factor having the opposite effect, Elgin carries the opposite alleles.
3. The fact that deficient lines XI, XVII and XIX produced disturbed ratios may indicate that these chromosomes carry modifying genes.

Conclusions Regarding the Use of Monosomic Analyses

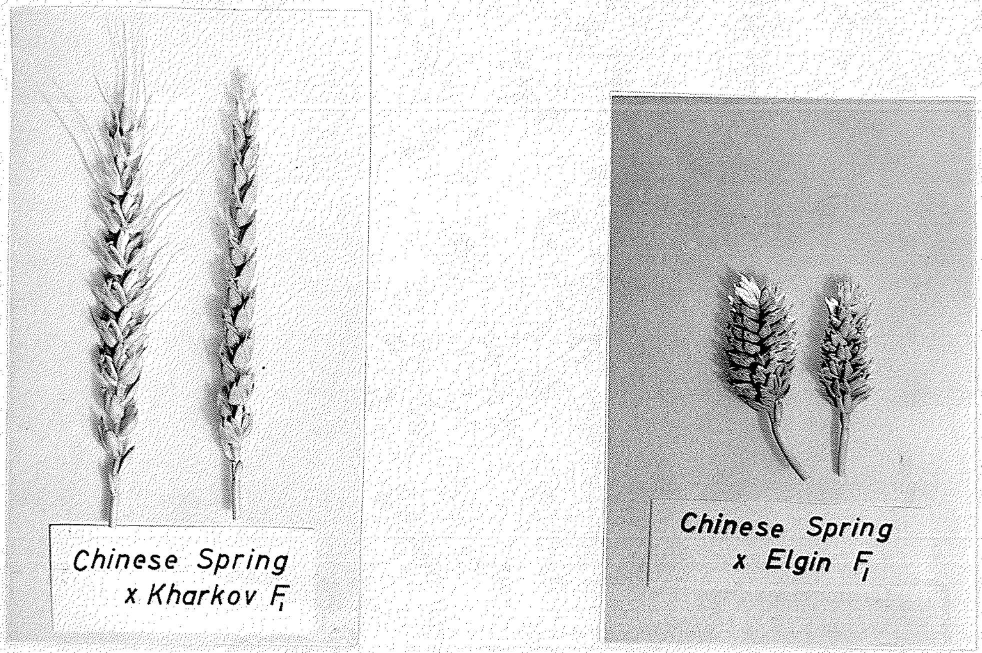
With respect to the general application of the monosomic analysis technique in determining the chromosomal location of specific genes, the author is of the opinion that its use is of major value in studying the inheritance of qualitative characters but that its use is very limited as regards quantitative characters that are strongly influenced by the environment. The application of the monosomic analysis technique is suitable for determining the location of the so-called major genes but is not suitable as a method of determining the location on modifying genes the effect of which are easily masked by environmental effects.

A second limitation of the monosomic analysis technique is the fact that the removal of a complete chromosome may cause a severe physiological upset, the effects of which could easily be regarded as being genetically controlled by factors on the particular missing chromosome. An error of this type could lead to numerous false conclusions regarding gene location and the mode of gene action.

Plate I Typical Spikes of the Parent Varieties and the F_1 Generations.



(a) Chinese Spring (b) (c) Kharkov



(d) (e)

Plate II Monosomic F_1 Spikes from the Crosses between 20 Chinese Spring Monosomics and Kharkov.

(a)

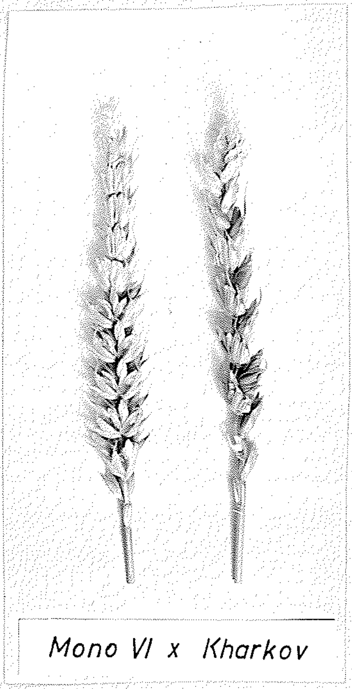
(b)

(c)

(d)

(e)

Plate II (continued)



(f)

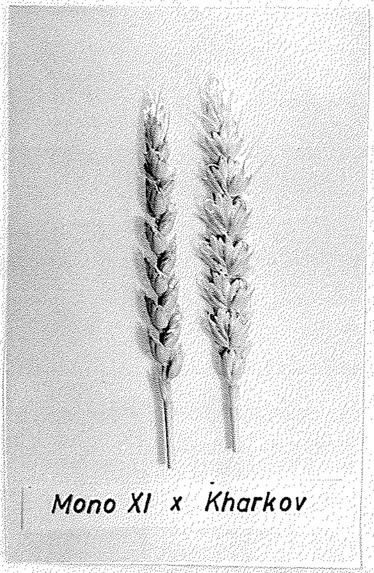
(g)

(h)

(i)

(j)

Plate II (continued)



(k)

(l)

(m)

(n)

(o)

Plate II (continued)

Mono XVI x Kharkov

(p)

Mono XVII x Kharkov

(q)

Mono XVIII x Kharkov

(r)

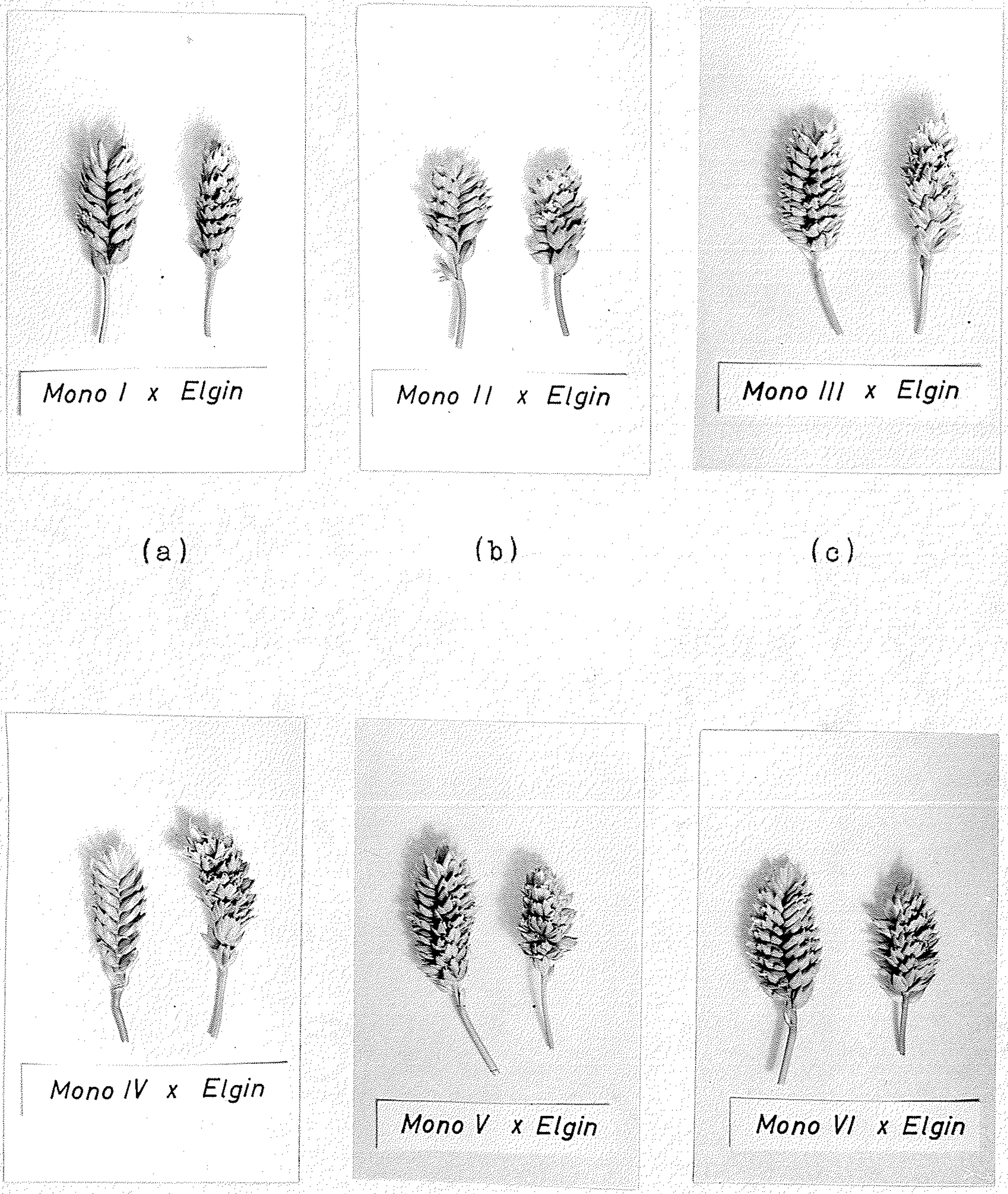
Mono XIX x Kharkov

(s)

Mono XX x Kharkov

(t)

Plate III Monosomic F_1 Spikes from the Crosses Between 19 Chinese Spring Monosomics and Elgin.



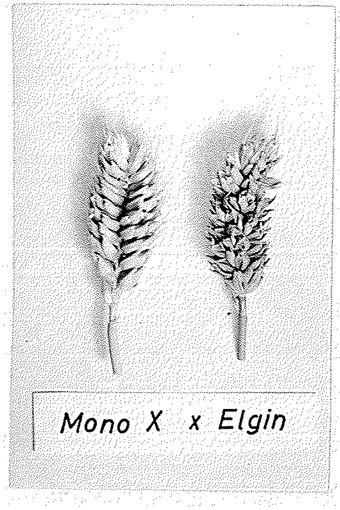
(a) (b) (c)

(d) (e) (f)

Plate III (continued)

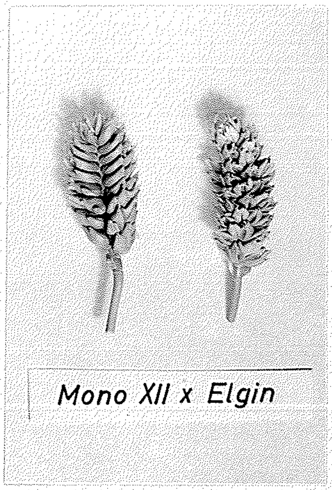
(g)

(h)

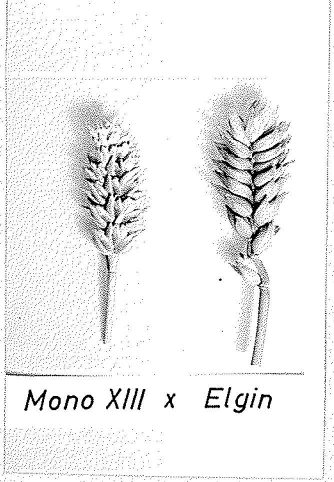


(i)

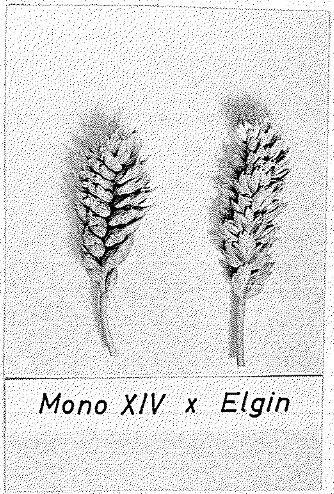
(j)



(k)

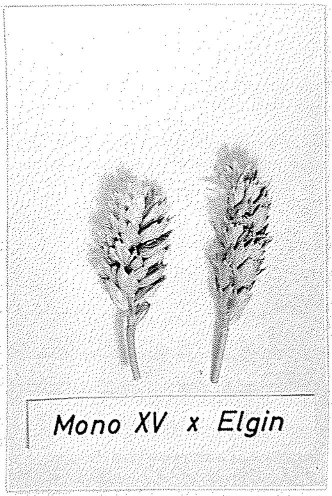


(l)

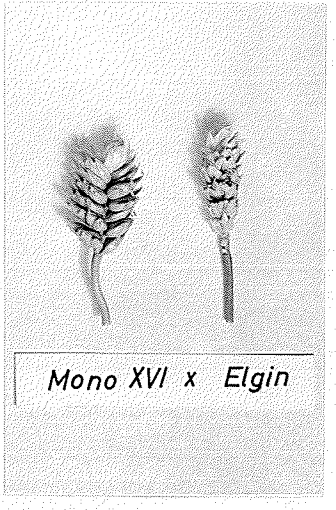


(m)

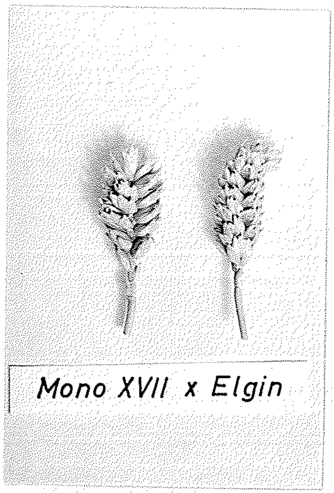
Plate III (continued)



(n)

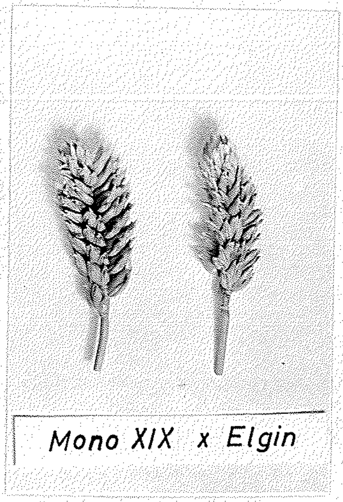


(o)

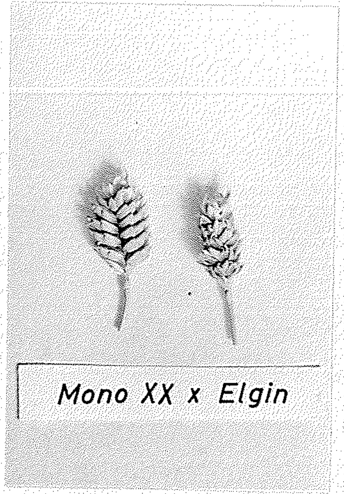


(p)

(q)



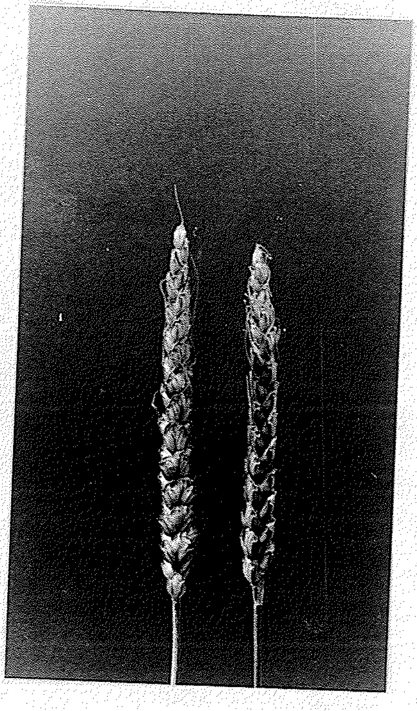
(r)



(s)

Plate IV Typical Spikes from each of the Segregation Classes Utilized in the Analysis of Awn Inheritance.

(a) Awnless



(b) Tip Awned

(c) Intermediate

(d) Half Awned

(e) Fully Awned

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