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STUDIES ON THE INHERITANCE OF, AND THE RELATION
BETWEEN CERTAIN PHYSIOLOGIC AND MORPHOLOGIC
CHARACTERS IN SEVERAL WHEAT CROSSES.

J.H. Torrie.

Department of Field Crops

University of Alberta,

April 1934.

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Department of Field Crops.

A THESIS

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TABLE OF CONTENTS.

	<u>Page.</u>
Introduction.....	1
Parental Material.....	3
General Methods.....	4
of	
Inheritance/Characters.....	6
Glume Color.....	6
Literature review.....	6
Methods and experimental results	8
Glume Pubescence	15
Literature review	15
Experimental results	15
Awning	17
Literature review	17
Experimental results	18
Spike Regularity	22
Methods and experimental results	22
Straw Color	25
Methods and experimental results	25
Seed Color	28
Literature review	28
Experimental results	29
Strength of Straw	35
Literature review	35
Methods and experimental results	36

Table of contents (continued).

	<u>Page.</u>
Height of Plant	43
Literature review	43
Methods and experimental results	44
Date of Heading	50
Literature review	50
Methods and experimental results	52
Grain Yield	59
Literature review	59
Methods and experimental results	60
Plumpness of Kernel	64
Literature review	64
Methods and experimental results	64
Texture of Kernel	74
Literature review	74
Methods and experimental results	76
Crude-protein Content	84
Literature review	84
Methods and experimental results	85
Relationship Studies Between the Characters	89
General	89
Tests of Independence or Association	90
Literature reviews	91
Awns and yield	91
Awns and straw strength	91
Experimental results	92

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Table of contents (continued).

	<u>Page.</u>
Correlation Studies	98
Plumpness and yield	98
Literature review	98
Methods and experimental results	99
Plumpness and growth period	100
Literature review	100
Methods and experimental results	101
Plumpness and crude-protein and texture	101
Literature review	101
Experimental results	102
Texture and crude-protein	103
Literature review	103
Experimental results	104
Yield, heading, height and lodging	106
Literature reviews.....	106
Yield and heading	106
Yield and height	107
Yield and lodging	107
Heading and height ,.....	108
Heading and lodging	108
Experimental results	108

Table of contents (continued).

	<u>Page.</u>
Economic Significance	111
Summary	112
Acknowledgment	117
References	118

STUDIES ON THE INHERITANCE OF, AND THE RELATION
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J.H. Torrie

INTRODUCTION

Drought is one of the major limiting factors of successful wheat production in western Canada. Every year some part of the prairie provinces suffers more or less from drought. Frequently large areas are very severely damaged, as was the case in the years 1930 to 1933. This shows the necessity of producing new wheat varieties more resistant to drought than the ones grown at present. Outside of the U.S.S.R. breeding for drought resistance has received little attention until recent years.

With this problem in view, crosses were made between several of the more drought resistant Russian varieties of spring wheat and the higher quality Canadian wheats. Although the principal object of this breeding program was to obtain varieties of spring wheat superior in drought resistance to those grown at present, the importance of other characters was not overlooked. Quality, as measured by texture of kernel and crude-protein content, was studied as well as

certain other important characters namely; earliness, strength of straw, yield and height. Such a study necessitated different environments which would act as differentials for the characters studied. Resistance to drought was studied at Brooks, in the dry area of Alberta. Quality was studied at Fallis, in the grey wooded soil area. The studies of earliness, strength of straw, yield and height were undertaken at Edmonton, in the black soil area. A description of these three soil types is given by Wyatt (70,71).

In conjunction with the above, studies were made on the inheritance of; glume color and pubescence, awning, spike regularity, straw color and seed color. In each case the characters were studied in relation to each other to see if any association existed.

PARENTAL MATERIAL

Crosses were made between the high quality varieties of Reward and Marquis and I-28-60 (Marquillo x Marquis-Kanred) a hybrid selection and two drought resistant Russian varieties of Caesium .0111 and Milturum .0321. All varieties belong to Triticum vulgare.

Reward C.A.N. 1509 (N.S.N. I-25-21) is a hard red spring wheat originating from^a Marquis x Prelude cross at the Central Experimental Farm, Ottawa(948). It was distributed for commercial growing in 1927. Reward is awnletted, has white pubescent glumes, irregular spikes and white, short, strong straw. It is early, fair in yield, non-drought resistant and possesses exceptionally good baking quality.

Marquis C.A.N. 1621 (N.S.N. I-0-9) originated at the Central Experimental Farm, Ottawa as a selection from a hybrid of Hard Red Calcutta x Red Fife (48). Marquis is awnletted, has white glabrous glumes, regular spikes, and white short to mid-tall, strong straw. It is mid-season in maturity, a good yielder, non-drought resistant and is the standard for baking quality.

Hybrid I-28-60 (Marquillo x Marquis-Kanred) was introduced from the University of Minnesota in 1928 and selected at the University of Alberta. I-28-60 is awnletted, has white glabrous glumes, regular spikes, and white short, strong straw. It is several days earlier than Marquis, a higher yielder, non-drought resistant and has good baking quality.

Caesium .0111 C.A.N. 1256 (N.S.N. I-28-20) was obtained from Dr. Talanov of the West Siberian Experimental Station in 1928 (64). Caesium is fully awned, has brown glabrous glumes, irregular spikes and purple tall, weak straw. It is late in maturity, a high yielder, drought resistant and possesses fair baking quality.

Milturum .0521 C.A.N. 1415 (N.S.N. I-28-14) was obtained from Dr. Talanov of the West Siberian Experimental Station in 1928 (64). Milturum is awnletted, has brown, glabrous glumes, regular spikes and white, tall, weak straw. It is late in maturity, a high yielder and drought resistant, but is poor in baking quality.

GENERAL METHODS.

The wheat crosses studied in this investigation were I-28-60 x Milturum, Reward x Caesium and Caesium x Marquis with its reciprocal. The crosses were made at Edmonton in 1929 and the F_1 plants grown in the field in 1930. There ^{were} ~~was~~ no indications of sterility in any of the crosses.

The material was grown in five-foot rows, one foot apart, with twenty-five seed per row, both at Edmonton in 1931 and 1932 and at Fallis and Brooks in 1932 and 1933. In 1933, at Edmonton, 10-foot rows, one foot apart, fifty seeds per row, were used. In all cases the parents were grown every thirty or fifty rows, or oftener, depending on the characters

studied. In all cases the F_2 plants were harvested individually. The F_3 lines of I-28-60 x Milturum, grown at Edmonton and Brooks were harvested on the individual plant bases, while at Fallis the plants in each F_3 row were bulked. All the plants of the F_3 of Reward x Caesium were harvested individually, however, with the reciprocal crosses of Caesium x Marquis, only a few of the F_2 populations were harvested in full for detailed study. The material grown at Fallis in 1933 was handled as in the previous year. Unfortunately the material grown at Brooks in 1933 was hailed out.

The F_2 of I-28-60 x Milturum were grown in the Genetic Nursery at Edmonton in 1931. The F_2 of Reward x Caesium and the reciprocal crosses of Caesium x Marquis were grown in 1932 at Edmonton.

The F_3 of I-28-60 x Milturum were replicated at Edmonton, Fallis and Brooks in 1932, while the F_3 of Reward x Caesium and the reciprocal crosses of Caesium x Marquis were sown at all three stations in 1933.

The F_4 selections of I-28-60 x Milturum were replicated at Edmonton, Fallis and Brooks in 1933.

The data obtained, from the classification of the material for the various characters for each F_2 population, originating from a different F_1 plant, were recorded separately and combined only when it was ascertained that there was no difference between the different populations. No significant differences, for any of the characters studied, were found in the reciprocal crosses of Caesium x Marquis. In measuring

variability, the standard deviation was used in the place of the coefficient of variability. It was found, that when a large difference existed in the mean of the parents, for a character like plant height, a small deviation from the mean in the shorter parent would give as great or^a greater coefficient of variability, than a larger deviation in the taller parent. Since it was considered desirable, in this investigation to express the variability in terms of the unit of measurement used for each character, the standard deviation was employed.

INHERITANCE OF CHARACTERS.

Glume Color

Literature review.

In the common wheats (Triticum vulgare), glume color has been classified as brown, red, yellow and white. However two classes are generally used, brown which includes various shades of brown and red; and white including the various shades of white and yellow.

Biffen (2), in 1905, found glume color to be governed by one factor pair. Brown glume was shown to be dominant over white glume. Howard and Howard (36) with a series of crosses between brown and white glumed wheats, report the F_1 to be intermediate and by the F_2 results showed a one factor differential. Clark, Quisenberry and Powers (14) with Hope x Hard Federation crosses state that glume color is inherited by a one-factor pair. Brown glume was shown to be dominant over white glume, however considerable variation was found to exist in the intensity of the brown color. The single factor hypothesis governing glume color in wheat has been reported also by the following workers (8, 9, 12, 19, 28, 38, 53, 54, 58, 60, 62).

Nilsson--Ehle (45) obtained a 15:1 ratio in crosses between white-chaffed and red-chaffed (brown) Swedish "landwheats". He explained his results by assuming that brown chaff color was controlled by two different factors, not necessarily of the same intensity and capable of cumulative effect, thus producing several shades of brown. Love and Craig (40) crossed a brown vulgare wheat with a yellow durum wheat and obtained in the F_2 a ratio of 15 brown to 1 yellow. Malinowski (41) in a brown spelta x brown vulgare crosses and Meyer (41) brown vulgare x a white compactum crosses both explain ^{color} glume / on a two factor pair basis.

Methods and experimental results.

In this investigation the inheritance of glume color was studied in the F_2 and F_3 generations of the crosses between I-28-60 x Milturum, Reward x Caesium and reciprocal crosses of Caesium x Marquis. Various shades of brown were noticed in the glume color of the hybrids, However, the plants were classified into two classes only, brown and white, as environment was believed to play a considerable part in the pigmentation of the glume.

In the I-28-60 x Milturum crosses, it was found that eight of the F_2 populations had a one factor difference, while seven had a two factor difference for glume color. These findings were substantiated by the F_3 data. Thus Milturum must possess two different genotypes for brown glume color. The data in tables 1 to 5 give the ratios and goodness of fits obtained for this character.

TABLE 1.

The breeding behavior of I-28-60 x Milturum F_3 lines
for glume^{color} and test^{of} goodness of fit to a theoretical
1:2:1 ratio.

CLASS	O	C	O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Brown	40	42.5	2.5	6.25	0.15
Segregating	88	85	3.0	9.00	0.11
White	42	42.5	0.5	0.25	0.01
	170	170.0		$\chi^2 = 0.27$	$P = 0.6065$

TABLE 2.

The breeding behavior of I-28-60 x Milturum, segregating F_3 lines for glume color and comparison with theoretical 3:1 ratio.

Class	o	c	Dev.	P.E.	Dev/P.E.	Odds.
Brown	1269	1283.25	14.25	12.04	1.18	1.35:1
White	442	427.75				

The data in tables 1 and 2 show very good fits for a ^{One-}factor difference.

TABLE 3.

The breeding behavior of I-28-60 x Milturum, F_3 lines for glume color and test of goodness of fit to a theoretical 7:4:4:1 ratio.

Class	o	c	o-c	(o-c) ²	$\frac{(o-c)^2}{c}$
Brown	86	73.08	12.92	166.93	2.28
Seg. 15:1	26	41.76	15.76	248.38	5.95
Seg. 3:1	43	41.76	1.24	1.54	0.04
White	12	10.44	1.56	2.43	0.23

$$\chi^2 = 8.50$$

$$P = 0.0376$$

ANNEX 1

Summary of the results of the survey conducted in the year 1970

The survey was conducted in the year 1970 and the results are summarized in the following table:

Summary of the results of the survey

Summary of the results of the survey				
Year	Number of respondents	Percentage of respondents	Percentage of respondents	Percentage of respondents
1970	100	100	100	100
1971	100	100	100	100
1972	100	100	100	100
1973	100	100	100	100
1974	100	100	100	100
1975	100	100	100	100
1976	100	100	100	100
1977	100	100	100	100
1978	100	100	100	100
1979	100	100	100	100
1980	100	100	100	100

The survey was conducted in the year 1970 and the results are summarized in the following table:

Summary of the results of the survey				
Year	Number of respondents	Percentage of respondents	Percentage of respondents	Percentage of respondents
1970	100	100	100	100
1971	100	100	100	100
1972	100	100	100	100
1973	100	100	100	100
1974	100	100	100	100
1975	100	100	100	100
1976	100	100	100	100
1977	100	100	100	100
1978	100	100	100	100
1979	100	100	100	100
1980	100	100	100	100

The survey was conducted in the year 1970 and the results are summarized in the following table:

The P value of .0376 indicates a poor fit to the theoretical 7:4:4:1 ratio. The reason for this is that there are too many apparently homozygous brown glume lines and too few lines segregating in a 15:1 ratio. This maybe accounted for because only 20 to 25 plants were grown in each F₃ row; had larger numbers been planted some of the brown lines would in all probability have showed a 15:1 segregation.

TABLE 4.

The breeding behavior of I-28-60 x Milturum segregating F₃ lines for^{glume}/color and comparison with a theoretical 15:1 ratio.

class	o	c	Dev.	P.E.	Dev/P.E.	Odds
Brown	660	665.62	5.62	4.35	1.3	1.6:1
White	50	44.38				

TABLE 5.

The breeding behavior of I-28-60 x Milturum segregating F₃ lines for glume color and comparison with a theoretical 3:1 ratio.

class	o	c	Dev.	P.E.	D/p.E.	Odds
Brown	936	945.75	975	10.34	.94	< 1
White	325	315.25

The data in tables 4 and 5 show that the segregating lines of these F_2 populations having a two factor differential for chaff color, in the F_3 give a very good fit for a one and two factor hypothesis respectively.

The brown glume of Caesium was found depended upon two-factor pairs, upon analyzing the F_2 and F_3 data the Reward x Caesium crosses and the reciprocal crosses of Caesium .0111 x Marquis.

TABLE 6.

The breeding behavior of Reward x Caesium F_3 lines for glume color and test of goodness of fit to a theoretical 7:4:4:1 ratio.

CLASS	o	c	o-c	$(o-c)^2$	$\frac{(o-c)^2}{c}$
Brown	53	57.3	4.3	18.49	0.32
Seg. 15:1	27	32.75	5.75	33.06	1.01
Seg. 3:1	38	32.75	5.25	27.56	0.84
White	13	8.2	4.8	23.04	2.81

$$\chi^2 = 4.98$$

$$P = 0.1735$$

The data in table 6 show a fair fit to the theoretical 7:4:4:1 ratio.

TABLE 7.

Breeding behavior of Reward x Caesium segregating F_3 lines for glume color and comparison with a theoretical 15:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Brown	988	992.8	4.8	53	0.91	<1
White	71	66.2				

The data in table 7 indicate a very good fit to the theoretical 15:1 ratio.

TABLE 8.

The breeding ~~and~~ behavior of Reward x Caesium segregating F_3 lines for glume color and comparison with a theoretical 3:1 ratio.

class	b	c	Dev.	P.E.	D/P.E.	Odds
Brown	1213	1209	4	11.73	0.34	<1
White	399	403				

The data in table 8 indicate a very good close fit to the theoretical 3:1 ratio.

TABLE 9.

The breeding behavior of reciprocal crosses of Caesium x Marquis F_3 lines for glume color and test of goodness of fit to a theoretical 7:4:4:1 ratio.

class	$\bar{O}$	$\bar{c}$	$O - c$	$(O - c)^2$	$\frac{(O - c)^2}{c}$
Brown	116	120.3	4.33	18.75	0.16
Seg. 15:1	68	68.76	.76	0.58	0.08
Seg. 3:1	66	68.76	2.76	7.62	0.11
White	25	17.19	7.81	61.00	3.55

$$\chi^2 = 3.90$$

$$P = .2245$$

The data in table 9 show a fairly good fit to the theoretical 7:4:4:1 ratio.

TABLE 10

The breeding behavior of reciprocal crosses of Caesium x Marquis segregating F_3 lines for glume color and comparison with a theoretical 15:1 ratio.

class	O	c	Dev.	P.E.	D/P.E.	Odds
Brown	2471	2504.06				
White	200	166.94	33.06	8.44	3.91	116:1

The data in table 10 do not give a good fit to the theoretical ratio. No explanation save that of chance can be offered for the occurrence of more white glume plants than

was expected.

TABLE 11

The breeding behavior of reciprocal crosses of Caesium x Marquis segregating F_3 lines for glume color and comparison with a theoretical 3:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Brown	2075					
White	655	682.5	27.5	15.29	1.80	3.5:1

The data in table 11 give a good fit to the theoretical 3:1 ratio. The data in tables 1 to 11 show that brown glume color is dominant over white. Caesium is shown to possess two-factor pairs for glume color, while Milturum is indicated as being heterogenous for this character, certain plants having one- while others two-factor pairs for the expression of brown glumes. The mode of inheritance of this character is in agreement with the results of other workers.

Glume Pubescence

Literature review.

Biffen (2) reported pubescent glume to be dominant to glabrous blume by one-factor pair. Kezer and Boyack (38), Love and Craig (40), Engledow and Hutchinson (16) and Meyer (41) substantiate the single factor hypothesis for pubescent glumes. Neatby and Goulden (43) in crosses between H-44-24 x Reward found a poor fit for a single factor difference, owing to the occurrence of too many glabrous lines in the F_3 . Howard and Howard (36) obtained a 15 pubescent to 1 glabrous ratio in the F_2 . From the F_3 behavior they concluded that two separate genes were responsible, "L" for long silky hairs and "S" for short hairs.

Experimental results.

In this investigation a 1-factor difference was obtained in the cross between Reward x Caesium for pubescence of glume.

TABLE 12.

The breeding behavior of Reward x Caesium F_3 lines for chaff pubescence and test of goodness of fit to a theoretical 1:2:1 ratio.

class	o	c	o-c	$(o - c)^2$	$\frac{(o - c)^2}{c}$
pubescent	30	32.5	2.5	6.25	0.19
Segregating	64	65.	1.0	1.00	0.02
Glabrous	36	32.5	3.5	12.25	0.38

$$P \approx 0.6065$$

$$\chi^2 = 0.59$$

The data in table 12 indicate an excellent fit to the theoretical 1:2:1 ratio.

TABLE 13.

The breeding behavior of Reward x ~~Caesium~~ segregating F_3 lines for chaff pubescence and comparison with a theoretical 3:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Pubescent	1808	1917.7	109.7	14.77	7.4	V.G.
Glabrous	749	639.3				

The data in table 13 show a poor fit to the theoretical 3:1 ratio. Too many glabrous plants were found in proportion to the pubescent plants. There was a considerable variation in the degree of pubescence, and in a number of cases it was difficult to distinguish between slightly pubescent and glabrous plants. It is also thought that the pubescence of a number of the slightly pubescent plants may have been brushed off during handling, thus making them appear glabrous. The same difficulty was found in classifying the F_2 , however when the F_2 data were corrected on the F_3 behavior a good fit resulted. In spite of the poor fit obtained in the segregating lines of the F_3 generation, it appears that in the Reward x ~~Caesium~~ crosses pubescent glume is partially dominant over glabrous glume by one factor pair.

The single factor hypothesis for glume pubescence is in agreement with the results of other workers. Neatby and Goulden (43) in crosses between H-44-24 x Reward obtained in the F_3 an excess of glabrous lines; a similar excess of glabrous plants was found in the segregating F_3 lines of Reward x Caesium.

Awning

Literature review.

The literature compiled on the inheritance of awns is very extensive. Considerable difference of opinion exists, as to methods of classification and ^{the mode of} inheritance of awns. The crosses in this study were between awnletted and fully awned wheats. Accordingly only the literature dealing with the crosses between similar awn types is reviewed to any extent.

Saunders (47) states that in crosses between awned and awnless wheats the F_1 is usually intermediate, which indicates incomplete dominance of awnless condition. Howard and Howard (36,37) crossed beardless and fully bearded wheats obtaining a two-factor differential. They also crossed two awnletted wheats from which they obtained the entire range of awns. Clark (9) in reciprocal crosses between Kota and Hard Federation suggest two main dominant factors with minor modifying factors governing awn expression. The fully awned condition was recessive.

Howard and Howard (36, 37) found a one-factor difference in crosses between awnletted and awned wheats. Harrington (28), in crosses between Hard Red Calcutta (bearded) and Taylor's Wonder (tip-awned) obtained a ratio of 3 tip-awns to 1 awned. The one-factor hypothesis with the awnletted condition dominant was substantiated by Clark and Quisenberry (13) in crosses between Marquis and Kota; Goulden, Neatby and Welsh (27) with Marquis x H-44-24 crosses; Goulden and Neatby (43) with Reward x H-44-24 crosses; and the following other investigators (24, 38, 46, 53, 54, 56, 57, 60, 61, 63). Kilduff (39) found a very poor fit for a 1-factor hypothesis in a Kota (awned) x Garnet (awnletted) cross, having obtained too many true breeding fully awned lines. He suggests that more than 1 factor is operating in this cross. Clark and Quisenberry (13) in a cross between Sonora (weakly awnletted) x Reliance (fully awned) reports in the F_3 too few awnletted lines and too many segregating lines. The segregating lines showed a great excess of awned plants which may be due to a dominant factor pair for the awned condition.

Experimental results.

The inheritance of awns was studied in reciprocal crosses of Caesium x Marquis and crosses of Reward x Caesium. In ^{the} ~~two~~ crosses the F_1 plants were intermediate, however they represented the awnletted parents ^{more} closely than the awned parent. The F_2 and F_3 were studied in detail in both crosses. The data obtained show that the awnletted condition is partially dominant and is governed by one main factor pair. The awnletted plants showed a considerable range in the degree of awn expression in both the F_2 and the F_3 . In figure 1 is shown the two awn classes with intermediate types.

FIGURE 1.

Awn classes with intermediate types.

TABLE 14.

The breeding behavior of Caesium x Marquis F_3 lines for awning and test of goodness of fit to a theoretical 1:2:1 ratio.

class	o	c	$\bar{d}-c$	$(o - c)^2$	$\frac{(\bar{d} - c)^2}{c}$
Awning	32	32.75	0.75	0.56	0.02
Segregating	70	64.50	5.50	30.25	0.47
Awningletted	29	32.75	3.75	14.06	0.43

$$P = > 0.6065$$

The data in table 14 show an excellent fit to the theoretical 1:2:1 ratio.

TABLE 15.

The breeding behavior of Caesium x Marquis segregating F_3 lines for awning and comparison with a theoretical 3:1 ratio.

class	o	c	Div.	P.E.	D/P.E.	Odds
awnletted	21 29	2164.5	55.3	15.67	2.27	6.96
Awning	7 57	721.5				

The data in table 15 show a good fit to the theoretical ratio of 3:1.

TABLE 16.

The breeding behavior of Reward x Caesium F_3 lines for awning and test of goodness of fit to a theoretical 1:2:1 ratio.

class	o	c	o - c	$(o - c)^2$	$\frac{(o - c)^2}{c}$
Awmed	86	74	12	144	1.95
Segregating	131	148	17	289	1.95
Awnletted	79	74	5	25	0.34

$$P = 0.2399.$$

The data in table 16 show a fair fit to the theoretical 1:2:1 ratio.

TABLE 17.

The breeding behavior of Reward x Caesium segregating F_3 lines for awning and comparison with a theoretical 3:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Awnletted	3782	3996				
Awmed	1546	1332	214	21.36	10.02	V.G.

The data in table 17 give a poor fit to the theoretical 3:1 ratio. The proportion of awnletted to awmed plants is too low. From an examination of the data in tables 14, 15 and 16 it will be found that the proportion of awmed

lines or plants to the expected is always too great. However only in table 17 is this discrepancy great enough to render the data nonsignificant in the light of its odds. No satisfactory explanation can be offered for this preponderance of awned individuals as it is very unlikely that awnletted plants would be classified as being awned. An examination of the data for each individual F_2 population showed that 13 out of 14 populations had too many awned plants. It is suggested that certain minor factor pairs modify the expression of the main factor pair for the awnletted condition to give a higher proportion of awned plants than would be expected with the one-factor hypothesis.

The single factor differential and the partial dominance of the awnletted condition is in agreement with the results of other investigations between crosses of awnletted and awned wheats.

Spike Regularity

Methods and Experimental results.

In the examination of the literature on inheritance in wheat no instance has been found reporting the inheritance of spike regularity. The spikelets in most common wheat varieties are arranged, more or less parallel to the rachis from a lateral view, giving a uniform appearance to the spike. In the case of Reward and Caesium most of the spikelets are arranged at a distinct angle to the rachis giving an unsymmetrical appearance to the spike. These two types of spikes are shown in figure 2.

FIGURE 2.

Irregular and regular spike.

This character was studied in the reciprocal crosses Caesium x Marquis in the F_2 and F_3 generations.

TABLE 18.

The breeding behavior of Caesium x Marquis F_3 lines for spike regularity and test ^{of goodness} of fit to a theoretical 1:2:1 ratio.

class	o	c	o - c	$(o - c)^2$	$\frac{(o - c)^2}{c}$
Irregular	56	73.75	17.75	315.06	4.27
Segregating	172	147.50	24.50	600.25	4.07
Regular	67	73.75	6.75	45.56	0.62

$$\chi^2 = 8.96$$

$$P = 0.0114$$

The data in table 18 show a poor fit to the theoretical 1:2:1 ratio.

TABLE 19.

The breeding behavior of Caesium x Marquis segregating F_3 lines for spike regularity and comparison with a theoretical 3:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Irregular	5027	5172	144	24129	5.93	V.G.,
Regular	1868	1724				

The data in table 19 show a poor fit to the

theoretical 3:1 ratio. Although poor fits were obtained for a one-factor hypothesis for the character of spike regularity, it is quite evident that no other hypothesis would fit the data obtained. Considerable difficulty was found in classifying certain plants probably due to an intermediate condition for this character resulting from partial dominance of the irregular spike.

Straw color

Methods and experimental results

In the examination of the literature on inheritance in wheat no instance has been found reporting the inheritance of straw color. Marquis and Reward have white straw while Caesium has purple straw. In the F_2 some difficulty was found in classifying the culms for straw color owing to a bleaching out, in certain plants, of the purple color. In the F_3 very little difficulty was found in this regard. Any plants of which the color of the culms was doubtful, the leaf sheath was pulled off thus uncovering a part of the culm which had not been exposed to the sunlight directly. By this method it was quite easy to distinguish the normal white culms from bleached purple culms. In both the Reward x Caesium and the reciprocal Caesium ~~Caesium~~ x Marquis crosses a one-factor difference was obtained with the purple straw dominant.

TABLE 20

The breeding behavior of Caesium x Marquis F_3 lines for straw color and test of goodness of fit to a theoretical 1:2:1 ratio.

class	o	c	o - c	$(o - c)^2$	$\left(\frac{o - c}{c}\right)^2$
Purple	83	73.75	9.25	85.56	1.16
Segregating	137	147.50	10.50	110.25	0.75
White	75	73.75	1.25	1.56	0.02

$$\chi^2 = 1.93$$

$$P = 0.13846.$$

The data in table 20 indicates a good fit to the theoretical 1:2:1 ratio.

TABLE 21

The breeding behavior of Caesium x Marquis segregating F_3 lines for straw color and comparison with the theoretical 3:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Purple	4317	42845	3.15	22.03	1.43	2:1
White	1397	14285				

The data in table 21 show a good fit to the theoretical 3:1 ratio.

TABLE 22

The breeding behavior of Reward x Caesium F_3 lines for straw color and test of goodness of fit to a theoretical 3:1 ratio.

class	o	c	o - c	$(o - c)^2$	$\frac{(o - c)^2}{c}$
Purple	28	33.0	5.0	25	0.76
Segregating	77	66.0	11.0	121	1.83
White	27	33.0	6.0	36	1.09

$\chi^2 = 3.68$
$P = 0.1631$

The data in table 22 show a fair fit to the theoretical 1:2:1 ratio.

TABLE 23.

The breeding behavior of Reward x Caesium segregating for straw color and comparison with the theoretical 3:1 ratio.

class	o	c	d	P.E.	D/P.E.	Odds
Purple	2401	2381.2	19.8	16.45	1.79	3.45:1
White	774	793.8				

The data in table 23 indicate a good fit to the theoretical 3:1 ratio.

Seed Color

Literature review.

Biffen (2) reports red color to be dominant over white in the F_1 and to segregate on a single factor basis in the F_2 . Nilsson-Ehle (45) in a series of crosses obtained one, two and three factor differences governing the inheritance of seed color in wheat. He states that he obtained varying shades of red and that this was due to the cumulative action of the several color factors. He was the first to obtain white seed plants from crosses between two red parents. Howard and Howard (36) in a series of crosses substantiate the one, two- and three-factor hypothesis of Nilsson-Ehle. Gaines (22) found three-factor pairs governing seed color and states that the factors are cumulative in nature resulting in various degrees of redness. Clark and Hooker (12) in reciprocal crosses of Hard Federation x Marquis found the red color of Marquis to be due to two-factor pairs in ten F_2 populations and to one factor pair in two F_2 populations. Hayes and Robertson (35) in a Marquis x Minturki-Kanred cross report three-factor pairs for seed color. They state that there was a variation in the color of the red segregates but that it was impossible to differentiate between the various classes. Kilduff (39) in a Kota x Red Bobs cross found that each parent carried a different factor pair for seed color. Numerous other workers (9, 14, 28, 60, 62, 63) have reported on one, two- or three-factor pairs governing the inheritance of seed color in wheat.

Experimental results.

The inheritance of seed color was studied in the F_2 and the F_3 of the crosses of Caesium with Marquis and Reward. Segregation was found on a 3-factor pair basis. Variation was noticed in the intensity of the red color of the hybrid kernels but it was found impossible to classify the material into different classes for degree of redness.

TABLE 24.

The breeding behavior of Caesium x Marquis F_2 plants for seed color and comparison with a theoretical 63:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	1457	1435.22	1.78	3.15	0.56	< 1
White	21	22.78				

The data in table 24 show a very good fit to the theoretical ratio.

TABLE 25

The breeding behavior of Caesium x Marquis F_3 lines for seed color and test of goodness of fit to a theoretical 37:8:12:6 ratio.

class	o	c	o - c	$(o - c)^2$	$\frac{(o - c)^2}{c}$	
Red	185	158.36	26.64	709.69	4.48	
Seg 63:1	23	34.24	11.24	126.34	3.69	$\chi^2 = 14.44$
Seg 15:1	37	51.36	14.36	206.21	4.01	$P = 0.0062$
Seg 3:1	22	25.68	3.68	13.54	0.53	
White	7	4.28	2.72	7.40	1.73	

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535	536	537	538	539	540
541	542	543	544	545	546
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559	560	561	562	563	564
565	566	567	568	569	570
571	572	573	574	575	576
577	578	579	580	581	582
583	584	585	586	587	588
589	590	591	592	593	594
595	596	597	598	599	600
601	602	603	604	605	606
607	608	609	610	611	612
613	614	615	616	617	618
619	620	621	622	623	624
625	626	627	628	629	630
631	632	633	634	635	636
637	638	639	640	641	642
643	644	645	646	647	648
649	650	651	652	653	654
655	656	657	658	659	660
661	662	663	664	665	666
667	668	669	670	671	672
673	674	675	676	677	678
679	680	681	682	683	684
685	686	687	688	689	690
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697	698	699	700	701	702
703	704	705	706	707	708
709	710	711	712	713	714
715	716	717	718	719	720
721	722	723	724	725	726
727	728	729	730	731	732
733	734	735	736	737	738
739	740	741	742	743	744
745	746	747	748	749	750
751	752	753	754	755	756
757	758	759	760	761	762
763	764	765	766	767	768
769	770	771	772	773	774
775	776	777	778	779	780
781	782	783	784	785	786
787	788	789	790	791	792
793	794	795	796	797	798
799	800	801	802	803	804
805	806	807	808	809	810
811	812	813	814	815	816
817	818	819	820	821	822
823	824	825	826	827	828
829	830	831	832	833	834
835	836	837	838	839	840
841	842	843	844	845	846
847	848	849	850	851	852
853	854	855	856	857	858
859	860	861	862	863	864
865	866	867	868	869	870
871	872	873	874	875	876
877	878	879	880	881	882
883	884	885	886	887	888
889	890	891	892	893	894
895	896	897	898	899	900
901	902	903	904	905	906
907	908	909	910	911	912
913	914	915	916	917	918
919	920	921	922	923	924
925	926	927	928	929	930
931	932	933	934	935	936
937	938	939	940	941	942
943	944	945	946	947	948
949	950	951	952	953	954
955	956	957	958	959	960
961	962	963	964	965	966
967	968	969	970	971	972
973	974	975	976	977	978
979	980	981	982	983	984
985	986	987	988	989	990
991	992	993	994	995	996
997	998	999	1000	1001	1002
1003	1004	1005	1006	1007	1008
1009	1010	1011	1012	1013	1014
1015	1016	1017	1018	1019	1020
1021	1022	1023	1024	1025	1026
1027	1028	1029	1030	1031	1032
1033	1034	1035	1036	1037	1038
1039	1040	1041	1042	1043	1044
1045	1046	1047	1048	1049	1050
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1057	1058	1059	1060	1061	1062
1063	1064	1065	1066	1067	1068
1069	1070	1071	1072	1073	1074
1075	1076	1077	1078	1079	1080
1081	1082	1083	1084	1085	1086
1087	1088	1089	1090	1091	1092
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1111	1112	1113	1114	1115	1116
1117	1118	1119	1120	1121	1122
1123	1124	1125	1126	1127	1128
1129	1130	1131	1132	1133	1134
1135	1136	1137	1138	1139	1140
1141	1142	1143	1144	1145	1146
1147	1148	1149	1150	1151	1152
1153	1154	1155	1156	1157	1158
1159	1160	1161	1162	1163	1164
1165	1166	1167	1168	1169	1170
1171	1172	1173	1174	1175	1176
1177	1178	1179	1180	1181	1182
1183	1184	1185	1186	1187	1188
1189	1190	1191	1192	1193	1194
1195	1196	1197	1198	1199	1200
1201	1202	1203	1204	1205	1206
1207	1208	1209	1210	1211	1212
1213	1214	1215	1216	1217	1218
1219	1220	1221	1222	1223	1224
1225	1226	1227	1228	1229	1230
1231	1232	1233	1234	1235	1236
1237	1238	1239	1240	1241	1242
1243	1244	1245	1246	1247	1248
1249	1250	1251	1252	1253	1254
1255	1256	1257	1258	1259	1260
1261	1262	1263	1264	1265	1266
1267	1268	1269	1270	1271	1272
1273	1274	1275	1276	1277	1278
1279	1280	1281	1282	1283	1284
1285	1286	1287	1288	1289	1290
1291	1292	1293	1294	1295	1296
1297	1298	1299	1300	1301	1302
1303	1304	1305	1306	1307	1308
1309	1310	1311	1312	1313	1314
1315	1316	1317	1318	1319	1320
1321	1322	1323	1324	1325	1326
1327	1328	1329	1330	1331	1332
1333	1334	1335	1336	1337	1338
1339	1340	1341			

The data in table 25 give a poor fit to the theoretical ratio. With a larger number of plants in each F_3 row it would be expected that certain of the red lines would segregate into a 63:1 ratio. The small number of lines segregating for the 15:1 ratio can hardly be explained on this basis, for the average population of each F_3 row was approximately 45 plants.

TABLE 26

The breeding behavior of Caesium x Marquis segregating F_3 lines for seed color and comparison with the theoretical 63:1 ratio

class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	916	901.33	8.33	2.56	3.25	30.1
White	23	14.67				

The data in table 26 indicate a fair fit to the theoretical ratio.

TABLE 27

The breeding behavior of Caesium x Marquis segregation F_3 lines for seed color and comparison with the theoretical 15:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	1355	1352.19	7.19	6.21	1.16	15:1
White	98	90.81				

The data in table 27 show a very good fit to the theoretical ratio.

TABLE 28

The breeding behavior of Caesium x Marquis segregating F_3 lines for seed color and comparison with the theoretical 3:1 ratio.

Class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	686	665.25	20.75	8.70	2.39	8.56:1
White	201	221.75				

The data in table 28 show a very good fit to the theoretical ratio.

TABLE 29

The breeding behavior of Reward x Caesium F_2 plants for seed color and comparison with the theoretical 63:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	129	129.94	194	.96	.98	< 1
White	3	2.06				

The data in table 29 show an excellent fit to the theoretical ratio.

TABLE 30

The breeding behavior of Reward x Caesium F_3 lines for seed color and test of goodness of fit to a theoretical 37:8:12:6:1 ratio.

cla ss	o	c	o - c	$(o - c)^2$	$\frac{(o - c)^2}{c}$
Red	89	76.31	12.69	161.04	2.11
Seg. 63:1	8	16.50	8.50	72.25	4.38
Seg. 15:1	21	24.75	3.75	14.06	0.57
Seg. 3 :1	11	12.38	1.38	1.90	0.15
White	3	2.06	0.94	0.88	0.43

$$\chi^2 = 7.64$$

$$P = 0.0553$$

The data in table 30 give a fair fit to the theoretical ratio. As in the case of Caesium x Marquis a larger number of plants per F_3 row would probably have resulted in certain of the red F_3 lines segregating into a 63 reds : 1 white ratio.

TABLE 31

The breeding behavior of Reward x Caesium segregating F_3 lines for seed color and comparison with the theoretical 63:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	333	335.67	2.67	1.54	1.731	3.2:1
White	8	5.33				

The data in table 31 show a very good fit to the theoretical ratio.

TABLE 32

The breeding behavior of Reward x Caesium segregating F_3 lines for seed color and comparison with the theoretical 15:1 ratio.

Class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	780	782.81	2.81	4.72	0.60	< 1
White	55	52.19				

The data in table 32 indicate a very good fit to the theoretical ratio.

TABLE 33

The breeding behavior of Reward x Caesium segregating F_3 lines for seed color and comparison with the theoretical 3:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Red	341	339	2	6.21	.32	< 1
White	111	113				

The data in table 33 show a very good fit to the theoretical ratio.

The data in tables 25 to 33 clearly indicate a three-factor difference for seed color in the crosses of Caesium with Marquis and Reward from which may be concluded that both Reward and Marquis possess two genes for red seed color, located on corresponding homologous chromosomes while Caesium possess one gene for red seed color, located on a third pair of chromosomes. In two of the F_2 populations of Caesium x Marquis with a population of over 1000 F_3 plants, no white seeded segregations were obtained.

This can be explained, if it is assumed that one of the factor pairs for red seed color of Marquis and the factor pair for red seed color of Caesium are located on corresponding homologous chromosomes.

The three-factor hypothesis for seed color in the above crosses is in agreement with the work of Nilsson-Ehle (45), Howard and Howard (36), Hayes and Robertson (35) and others. Various shades of red were noticed among the red seeded segregation but it was impossible to separate the plants into different

classes for red, depending upon the number of factor pairs present for red color, as was done by Nilsson-Ehle (45). The data support the conclusion of Hayes and Robertson (35) that Marquis has two pairs of independantly inherited factors for seed color.

Strength of Straw

Literature review.

In wheat strength of straw is a character of great economic importance. Its study in a hybrid population, particularly where one of the parents is inclined to be weak, ranks of first importance. Resistance to lodging is a character which is greatly influenced by environment, consequently a genetic interpretation of its inheritance is difficult. As yet very little work has been done on the study of this character.

Howard and Howard (36) state that standing power (resistance to lodging) is dependent upon strong straw and a well developed root system. In crosses between A 88, a strong strawed variety with an inferior root system, and Pusa 22, a weak strawed variety with a strong root system, they obtained in the F_2 all possible recombinations.

Harrington (29) studied erectness in two durum crosses, Kubanka 8 x Pentad and Mindum x Pentad. He reports transgressive segregation in both crosses in both directions for straw strength. His material in the F_4 was grown in duplicate, correlating between the two series he obtained in the case of the Mindum x Pentad a correlation of $+0.389 \pm 0.037$ and in the Kubanka x Pentad

a correlation of $+0.573 \pm .0041$. He suggests correctness is controlled by several heritable factors, part coming from each parent.

Waldron (68), in a Kota x Marquis cross found differences in straw strength of the selections made, one of which was considerable weaker than Kota, the weaker parent; which indicated that transgressive segregation for straw strength had occurred.

Kilduff (39) studied the strength of straw in Kota crossed with Red Bobs and Garnet. He concluded that the complex segregation obtained could be best explained on a multiple factor basis, the presence of two main factors being indicated. A partial dominance of the weak straw of Kota was obtained.

Methods and experimental results.

Lodging was studied in the F_3 of reciprocal crosses of Caesium x Marquis and Reward x Caesium. The material was grown on a block of land which had been down to fallow for two years. A very good differential for lodging occurred. The lodging notes were taken just prior to harvest.

A lodging index was calculated for each F_3 row. This index was based upon the percentage of plants lodged and the average angle off the vertical. 0 indicates no lodging while 100 represents complete lodging. The index was obtained by the formula percentage of plants lodged x angle off the vertical

TABLE 34

Frequency distribution of Caesium x Marquis F_3 lines and parental rows for lodging index, grown at Edmonton in 1933.

Parent or cross	Lodging index in 5% classes												Mean	S.D.
	0	3	8	13	18	23	28	33	38	43	48	53		
Caesium								5	5	8	5	7	43.65+0.86	6.95+0.60
Marquis	7	20	20	1									2.97+0.33	2.66+0.23
F ₃ hybrids	30	154	240	207	224	169	100	116	60	27	41	26	18.90+0.25	13.65+0.17

The difference between two parent of 40.68±0.97 is very significant.

The data in table 34 show that the average index of the F_3 lines is approximately midway between that of the two parents, being somewhat closer to the mean of Marquis than Caesium. The variability of the F_3 lines as expressed by the standard deviation was greater than the variation in the most variable parent Caesium, the difference being 6.70±0.29.

FIGURE 3.

Curves showing the distribution of Caesium x Marquis F₃ lines and parental rows, for lodging index, grown at Edmonton in 1935.

Figure 3 shows in graphical form the distribution of Caesium x Marquis F_3 lines and parental rows for the lodging index. The lodging index is expressed in 5% classes along the horizontal axis while the per cent. of the population is shown along the vertical axis. The per cent. of the population of the parents is expressed on a smaller scale than that of the hybrids.

TABLE 35

The breeding behavior of Caesium x Marquis F_3 lines for strength of straw and comparison with the theoretical 3:1 ratio.

Class	o	c	Dev.	P.E.	D/P.E.	Odds
Strong straw.	1024	1045.5	21.5	10.88	1.97	5:1
Weak straw.	370	348.5				

A distinct break occurs in the curve at class 28 for the lodging index as shown in figure 3. Taking this point as an arbitrary dividing place, a good fit to a 3:1 ratio is shown by the data in table (35). The data in table (35) indicate one main factor, with partial dominance of strong straw, governing straw strength; however, it is believed that there is also a number of minor modifying factors influencing lodging in Caesium x Marquis.

TABLE 36

Frequency distribution of Reward x Caesium F₃ lines and parental rows for the lodging index grown at Edmonton in 1933.

Parent or cross	Lodging index in 5% classes										Mean	S.D.
	0	3	8	13	18	23	28	33	38	43		
Caesium								2	6	4	38.85±0.44	2.30±0.32
Reward	3	9									2.25±0.25	1.30±0.18
F ₃ hybrids	11	42	24	17	14	7	6	2	5	4	11.55±0.67	11.35±0.47

The difference between the two parents of 36.60±0.36 is very significant. The data in table (36) show that the average index of the hybrid rows is closer to that of the Reward than the Caesium parent which indicates a partial dominance of the strong straw of Reward. The variability of the F₃ hybrid lines is considerably greater than that of the most variable parent Caesium, the difference being 8.05±0.57.

Figure 4 shows in graphic form the distribution of Reward x Caesium F₃ lines and parental rows for the lodging index. The figure was constructed in a similar manner to that for the Caesium x Marquis crosses. A distinct break occurs at 33 class for the lodging index. Taking this point as an arbitrary dividing place; a good fit to a 15 to 1 ratio is obtained as shown by the data in table 37.

FIGURE 4.

Curves showing the distribution of Reward x Caesium F_3 lines and parental rows, for lodging index, grown at Edmonton in 1933.

TABLE 37

The breeding behavior of Reward x Caesium F_3 lines for strength of straw and comparison ^{with} the theoretical 15:1 ratio.

class	o	c	Dev.	P.E.	D/P.E.	Odds
Strong straw	121	123.75				
Weak straw	11	8.25	2.75	3184	0.72	< 1

The data indicate two main factor pairs with possible modifying factors governing lodging in Reward x Caesium.

The presence of two main factors and indication of minor factors in Reward x Caesium is in agreement with the results obtained by Kilduff (39). However, Kilduff's work shows a partial dominance of weak straw, while in the present investigation strong straw is shown to be partially

dominant. This difference is probably ~~partly~~ ^{in part} due to the different parents used and also ^{to the fact} that the material was grown under different environments. Both Harrington (29) and Waldron (68) report transgressive segregation occurring for straw strength, however in the present study no indication of this was obtained.

Height of Plant

Literature review.

Freeman (20) in crosses between Sonora, a short vulgare wheat, with Algerian a tall durum wheat and a tall red vulgare wheat, found the average of the F_1 to be taller than either parents. In certain other crosses he found the F_1 to be intermediate between the two parents. In the F_2 a wide segregation for height occurred which suggested the presence of several factor pairs.

Clark (9) in reciprocal crosses of Kota x Hard Federation in the F_2 found tallness to be partially dominant. F_3 results, at Mandan, N.D. grown under drought conditions, indicate a reversal of the F_2 findings. He concludes that tallness may be partially dominant but due to heterosis is easily influenced by different environmental conditions.

Harrington (28), in Mindum x Pentad in the F_4 reports a significant correlation between two nurseries for height. Transgressive segregation occurred for shortness which indicates that more than 1-factor pair is present.

Clark and Hooker (12) in reciprocal crosses of Marquis x Hard Federation found that the F_2 to be intermediate between the parents and much more variable. In the F_2 and F_3 all gradations were found between the parents in average height, without significantly greater variability than the parents, which suggest that height is controlled by multiple factors.

Stewart (51) using Federation x Sevier found greater

variability in the F_3 than in either parent which indicates segregation, the exact nature of which was not determined.

Stewart and Heywood (58) with Federation x Sevier-Dicklow found a high correlation between the F_2 and F_3 . The distribution of the hybrids was that of a normal curve, which they state indicates segregation but not the nature of inheritance.

Methods and experimental results.

The F_3 of the crosses of Caesium with Marquis and Reward were studied for height. The criterion of height was ^{taken} as the distance from the base of the longest ^{culm} ~~awn~~ to the tip of the spike, excluding awns. The plants were measured individually, in centimeters, while being classified for other characters.

The data in table 38 give the frequency distribution of the mean height in three centimeters classes for the Caesium x Marquis F_3 lines and parental rows together with their mean and standard deviation.

These data are presented in graphical form in figure (5). In both figures 5 and 6 the horizontal axis gives the height in centimeters in classes of three centimeters while the vertical axis gives the per cent. of population in each class. A smaller scale was used for the parents for per cent. of population.

FIGURE 5.

Curves showing the distribution of Caesium x Marquis F₃ lines and parental rows, for plant height, grown at Edmonton in 1933.

TABLE 38

Frequency distribution of Caesium x Marquis F_3 lines and parental rows for height of plant in three centimeter classes grown at Edmonton in 1933.

parent or cross	Mean height in 3 cm. classes.												Mean	S.D.
	107	110	113	116	119	122	125	128	131	134	137			
Marquis	1	3	6									114.50+0.43	2.01+0.50	
Caesium					1	0	4	3	2			132.50+0.72	3.36+0.51	
F ₃	1	2	8	21	44	67	70	56	18	8	2	123.56+0.19	4.98+0.14	

The difference between the two parents of 18.0+ .49 is very striking. The variability of the F_3 lines is much greater than that of either parent which definitely indicated segregation. The mean of the F_3 , unlike that for Reward x Caesium is exactly midway between that of the two parents, which makes it difficult to state whether tall or short straw is partially dominant. The mean of one F_3 line was found taller than the Caesium parent, which indicates that transgressive segregation is not a factor in these crosses. Height in this cross can only be explained on the cumulative polymeric factor bases.

The data in table 39 give the frequency distribution of the mean heights in three centimeter classes for the Reward x Caesium F₃ lines and parental rows together with their mean and standard deviation .

TABLE 39

Frequency distribution of Reward x Caesium F₃ lines and parental rows for height of plant in three centimeter classes, grown at Edmonton in 1935.

Parent or cross	Mean height in 3 cm. classes												Mean	S.D.
	104	107	110	113	116	119	122	125	128	131	134	137		
Reward			3	8	1								112.49+0.33	1.71+0.24
Caesium .0111									1	9	2		131.24+0.29	1.50+0.21
F ₃ hybrids	1	1	0	1	4	12	32	25	26	16	11	2	125.53+0.32	5.43+0.23

FIGURE 6.

Curves showing the distribution of Reward X Caesium F_3 lines and parental rows, for plant height, grown at Edmonton in 1933.

The data in table 39 are presented in graphical form in figure 6.

The difference between the parents of 18.75 ± 0.54 cms. is very great. The variability of the F_3 lines compared with that of the parents is much greater, which definitely indicated that segregation has occurred. The average height of two F_3 lines are taller than that of Caesium while two are shorter than Reward, indicating slight transgressive segregation. The mean of the hybrids tends towards that of Caesium, the tall parent, thus indicating partial dominance of tallness. The variability of each F_3 line was studied by means of the standard deviation. It was found that apparently homozygous lines occurred at various points in the range. The data presented suggest that height in these crosses is controlled by a number of cumulative polymeric factors with partial dominance of tallness.

The polymeric factor hypothesis for height of plant is in agreement with that reported by other workers. Tallness is indicated as being partially dominant in Reward x Caesium which is in agreement with the results of certain of the crosses made by Freeman (20) and the F_2 of the Kota x Federation crosses of Clark's (9). Harrington (28) in durum crosses found shortness partially dominant.

Date of Heading

Literature Review.

Biffen (2) in an interspecific cross between Polish, an early wheat, and Rivit, a late wheat, reports the F_1 intermediate and a 1:2:1 segregation in the F_2 . Nilsson-Ehle (41) and later Tschermak (41) observed earliness to prevail in the F_1 , obtaining in the F_2 a complex segregation. Fruwirth cited by Florell (18) states earliness to be dominant to lateness in wheat.

Thompson (65,66,67) made a series of crosses, using eight varieties of vulgare wheat, some differing only slightly, and others differing widely, with regard to heading and ripening periods. He found that the F_1 approached the late parent in maturity and believed that the apparent dominance of lateness was due to hybrid vigor. In the F_2 he obtained a normal curve with an intermediate mean. He states transgressive segregation occurred where the parents differed only slightly. He concludes that earliness is controlled by a number of multiple factors and that many factors not concerned directly with earliness have an effect on maturity. He reports no instance of linkage with other characters.

Freeman (20) in crosses between two vulgare wheats and a durum x vulgare cross differing widely in heading period found the F_1 and F_2 to have an intermediate range with the mean nearer the late parent. Transgressive segregation was noted in the durum x vulgare cross. His hypothesis is that heading is controlled by at least 3-factor ^{Pairs} with late heading being partially dominant.

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Bryan and Pressley (6) in Sonora x Turkey report the F_1 to be intermediate in heading; in the F_2 slight transgressive segregation occurred with the mean inclined towards the late parent. In the F_3 and F_4 homozygous early, intermediate and late lines were obtained.

Florell (18) in Marquis x Sunset concluded earliness to be dominant by one factor pair with possibly a number of minor modifying factor pairs.

Clark (9) in reciprocal crosses of Kota x Hard Federation ~~concludes~~ earliness as determined by date of heading to be dominant. Harrington (29) in two durum crosses reports significant correlation in the F_4 between date of heading in replicate plantings in two separate nurseries. Transgressive segregation was obtained, which indicates ^{that} more than one-factor pair is responsible. Clark and Hooker (12) studied maturity in reciprocal crosses of Marquis x Hard Federation. In the F_2 and F_3 the hybrids were much more variable than either parent; transgressive segregation for lateness occurred. They obtained large positive correlations between the F_2 and F_3 for the heading and ripening periods.

Stephens (50) made extensive studies of earliness between early and late varieties using date of heading as the criterion of earliness. Reward, Prelude and Master were used as the early parents and Dicklow, Marquis and Federation as the late parents. The F_1 and F_2 were intermediate with a tendency towards the early parent.. The F_2 showed considerable more variation than the parents and tended toward a normal curve in distribution. In the F_3 of the Dicklow x Prelude, he obtained apparently homozygous families at nearly every

point in the range. His results show that earliness is due to a number of independent multiple factors having a cumulative effect. Florell (18) in back crosses between Quality x Little Club and Quality and Jenkins states, that three or more factor pairs are responsible for the difference in earliness, and that both parents contribute dominant factor pairs.

Methods and experimental results.

Environmental as well as ~~genetical~~ factors play an important role in determining the maturity of wheat varieties. Date of heading is probably less influenced by environment than is date of maturity in any given season and hence is a better indication of earliness/^{for}genetical studies. The emergence of the spike from the sheath was used as the index of heading. Heading was studied only in the F_3 of the Reward x Caesium crosses and reciprocal crosses of Caesium x Marquis. During the heading period the weather was ideal, no heavy rains occurring to prevent **daily notes** from being taken. In the Reward x Caesium crosses with one-half of the population, the plants were tagged daily as they headed, in the rest of the population the total number of plants headed per row were counted daily. The distribution of each F_3 line was expressed as the number of days from emergence to heading, and from this the mean and standard deviation of each line was calculated.

In the reciprocal crosses of Caesium x Marquis the date when the first plant, fifty per cent. of the plants and the last plant headed were taken, from which the mean number

of days from emergence to heading was calculated for each P_3 line. This last method, of obtaining the average heading date for an F_3 line, was checked by using it to calculate the mean date of heading for the F_3 Reward x Caesium lines. The two methods checked very closely.

In Reward x Caesium the variability of each F_3 line was calculated by means of the standard deviation in order to estimate the homozygosity of each line. Those lines having a standard deviation equal to or less than the average standard deviation for the most variable parent were considered to be homozygous.

TABLE 40

Frequency distribution of Reward x Caesium F_3 lines and parental rows, for date of heading, grown at Edmonton in 1953.

Parent or cross	No. of days from emergency to heading												Mean	S.D.
	51	52	53	54	55	56	57	58	59	60	61	62		
Reward	3	6	3										52.00 $\pm$ 0.14	0.71 $\pm$ 0.10
Caesium										9	3		61.25 $\pm$ 0.09	0.44 $\pm$ 0.06
F_3 lines	4	7	19	23	29	18	14	10	4	3	1		56.11 $\pm$ 0.12	2.08 $\pm$ 0.12

The data in table 40 give the distribution of the average of the parental rows and the F_3 lines of Reward x Caesium expressed in number of days from emerging to heading.

The average of each F_3 line should give a close approximation to the behavior of the F_2 plant from which it originated. The difference of 4.11_0.18 days between the two parents is significant. The difference in the variability of 1.37_0.16 between the hybrid lines and Reward the most variable parent is very great, clearly indicating segregation. In the F_3 distribution the parental extreme was reached in the case of the Caesium parent, but failed to be reached by one day the extreme of the Reward parent. Such a distribution indicated that no transgressive segregation occurred. The mean of the hybrids is more or less intermediate between that of the parents but tends towards the earlier parent indicating a partial dominance of earliness.

In figure 7 is given in graphical form the distribution of the mean for the parental rows and the F_3 lines for the number of days from emergence to heading. In figures 7 and 8 the number of days from emergence to heading is expressed along the horizontal axis while the per cent. of the population in each heading class is shown along the vertical axis, two scales being used, the smaller for the parents. The distribution of the F_3 lines gives a normal curve with a tendency towards the early parent. In comparing the standard deviation of the F_3 lines and the parental rows a number of F_3 lines were found to have variability equal to or less than the average variability of the most variable parent, at different points along the curve. This fact and the normal curve obtained for the average distribution of the F_3 lines, with a tendency towards the early parent, indicates that this character is controlled by a number of polymeric factors with a partial dominance of earliness.

FIGURE 7.

Curves showing the distribution of Reward x Caesium F_3 lines and parental rows, for date of heading, grown at Edmonton in 1933.

TABLE 41

Frequency distribution of Caesium x Marquis F_3 lines and parental rows, for date of heading, grown at Edmonton in 1933.

Parent or	No. of days from emergence to heading																Mean	S.D.
	52	53	54	55	56	57	58	59	60	61	62	63	64	65				
cross																		
Caesium								1	5	9	12	3					60.37 $\pm$ 0.12	0.94 $\pm$ 0.08
Marquis				1	4	13	12										57.20 $\pm$ 0.10	0.79 $\pm$ 0.07
F_3 lines	5	35	97	186	280	278	224	150	76	37	24	16	3	1			57.02 $\pm$ 0.04	2.11 $\pm$ 0.03

The difference between the two parents of 3.17 $\pm$ 0.16 days is very significant. The difference of 1.17 $\pm$ 0.09 between the variability of the F_3 hybrid lines and the most variable parent is very significant which indicates segregation. The mean of the hybrid lines is approximately the same as that of the early parent.

The distribution of the F_3 lines for given by the data in table 41 show that transgressive segregation occurred far beyond the extremes of both parents. This is clearly shown in figure 8. In Reward x Caesium the reason

FIGURE 8.

Curves showing the distribution of Caesium x Marquis F₃ lines and parental rows, for date of heading, grown at Edmonton in 1933.

why no transgressive segregation occurred is probably that any factor for earliness that Caesium may have is also found in the Reward parent. These data indicate that in Caesium x Marquis earliness^{is} partially dominant being controlled by several polymeric factors each parent contributing to this earliness.

A review of the literature on earliness in wheat shows considerable disagreement as to whether earliness or lateness is the dominant condition. Such disagreement is to be expected in crosses between different varieties. The data, in both the crosses studied, show a partial dominance of earliness which is in agreement with the works of Fruwith (18), Florell (18), Clark (9) and Stephens (50); on the other hand Thompson (65, 66, 67), Freeman (20) and Bryan and Pressley (6) report lateness to be partially dominant. The polymeric factor hypotheses, as indicated by the present work, is supported by most of the above workers. The lack of transgressive segregation in the Reward x Caesium crosses in which the parents differ greatly in maturity, and the presence of transgressive segregation in the Caesium x Marquis crosses, in which the parents differ only a few days in maturity supports the findings of Thompson (65, 66, 67).

Grain yield

Literature review.

Clark (9) states "yield may be considered as a character complex affected by environment and by most of the morphologic and physiological characters of the plants."

In reciprocal crosses of Kota x Hard Federation he found that while the F_2 was more variable than the parents the F_3 selections showed less variability. The average yield of both the F_2 and the F_3 tended towards the mean of Kota, the higher yielding parent. He states that yield appears to be governed by multiple factors.

Clark and Hooker (12) report from reciprocal crosses of Marquis x Hard Federation that the F_2 yield at Bozeman exceeds those of both parents and were less variable. Selected F_3 strains from high yielding F_2 plants significantly out-yielded both Marquis the high yielding parent at Bozeman and Hard Federation the high yielding parent at Harve, thus showing transgressive segregation. Significant positive correlations between the F_2 and F_3 yield at both Bozeman and Harve were obtained. However no correlation was obtained between the F_2 yield at Bozeman and the F_3 yield at Moccasin, which shows the great influence different environments have on yield.

Clark, Florell and Hooker (11) in crosses between Propo, Hard Federation and Bobs, in the F_2 found the average yield of the hybrids were between those of the parents. Nonsignificant correlations were obtained between the F_2 and the

F_3 yields in each cross. A number of F_3 strains in all crosses were found to exceed the best parental check rows in yield. Waldron (68) working with hybrid selections of Marquis x Kota obtained transgressive segregation due to the additive effects of high yielding factor pairs from both parents.

Clark and Smith (15) with a Nodak x Kahla crosses found that the average F_3 yield was inclined towards the higher yielding parent; transgressive segregation for higher yielding lines was observed.

Clark and Quisenberry (13) in Marquis x Kota crosses report the F_2 and F_3 more variable than either parent. Clark and Quisenberry and Powers (14) in Hope x Hard Federation crosses found the average F_3 to yield higher than either parent. They offered no genetic explanation.

Methods and experimental results.

The plant yield of grain in grams was determined on 57 F_3 rows of Reward x Caesium and 5 rows of each parent. Each ten-foot row contained approximately 40 to 45 spaced plants. The plants in each row were pulled separately and the heads wrapped in cheese cloth to prevent loss in handling. The border plants in each row were noted and were not used in this study. Each plant was threshed separately and the grain weighed in grams. The average grain yield per plant for each row was calculated. The data in table 42 give the frequency distribution of the average grain yield in grams for the parental varieties and F_3 lines of Reward x Caesium.

TABLE 42

Frequency distribution of Reward x Caesium F_3 lines and parental rows, for average grain yield in grams, grown at Edmonton in 1953.

Parent or	Grain yield in grams											S.D.
	Mean											
cross	5.8	6.3	6.8	7.3	7.8	8.3	8.8	9.3	9.8	10.3	10.8	
Reward		2	2	1								6.70+0.07 0.57+0.05
Caesium										1	3	10.50+0.10 0.32+0.07
F ₃ lines	1	1	6	13	11	11	6	5	2	1		7.97+0.08 0.93+0.06

The data in table 42 are presented in graphical form in figure 9. The grain yield in grams is shown along the horizontal axis while the per cent. of the population in each yield class is given along the vertical axis; two scales being used, the smaller for the parents.

FIGURE 9.

Curves showing the distribution of Reward x Caesium F₃ lines and parental rows, for grain yield per plant, grown at Edmonton in 1933.

The difference between the two parents of 3.8 ± 0.12 grams is very significant. The F_3 show considerable more variation than the parents. The distribution of the F_3 lines approaches that of a normal curve with a skewing toward the Reward parent. The parental extreme of the low yielding Reward parent was exceeded by one of the F_3 lines, however none of the F_3 lines reached the extreme of the high yielding Caesium parent. This indicates that no transgressive segregation has occurred. The distribution of the individual plant grain yields of the parental rows showed as much variable as the hybrid lines. However as shown by the data in table 42, when the average of the parental rows was taken, the variation was small as compared with the hybrids. Yield of grain in these crosses was indicated as being controlled by a large number of polymeric factors with a partial dominance of low yield.

The polymeric factor hypothesis for grain yield is in agreement with that reported by other workers. The low yield of the Reward parent is indicated as being partial dominant, which is in disagreement with the results reported by Clark and his^{co} workers (9, 12, 14, 15) who found high yield partially dominant. This difference is probably due to the different parents that were used and that the material was grown under a different environment.

Plumpness of Kernel

Literature review.

Hayes (30) using Marquis x Preston crosses states that kernel plumpness is an inheritable character, having obtained significant correlations between the F_3 and F_4 . The awned families were higher in per cent. of plump kernels than the awnless families.

Methods and experimental results.

Hayes (30) states that kernel plumpness is a good indication of the seasonal conditions which prevailed during that year. The F_3 lines of I-28-60 x Milturum were grown at Brooks in order to test their reaction under drought conditions. Since it was impossible to be at Brooks and study the growing material it was essential that some kernel character be studied in order to show the reaction of the hybrids to drought. Plumpness of the kernel was chosen for this purpose.

It was found that Milturum produced a plump sample of grain, while the kernels of I-28-60 were invariably shrivelled. The F_3 hybrids ranged between the two parents. Several methods of measuring plumpness of kernel were studied to find out which would give the best index. Weight per thousand kernels is a figure often used as an indication of plumpness and kernel size. It does not however always differentiate between these two characters.

It is also a laborious method involving considerable time and expense. A method of obtaining an indication of kernel plumpness was developed which is quite comparable to the usual "weight per measured bushel." The measured weight of each individual plant was obtained by taking a volume which would give a value in grams approximately the same as the weight per measured bushel in pounds. This was determined in a C.C. graduate to be about the weight in grams of 4.1 C.C. of grain times twenty. The graduate was cut off at this point and was used for obtaining weight per bushel. The grain was poured into the measure from a coin envelope, pressed lightly with the thumb and then levelled off with a scalpel drawn across the top of the measure.

In order to compare the accuracy of the small measure with the usual weight per bushel equipment (pint measure), weights per measured bushel were determined on 184 samples of spring wheat. Four determinations were made with the graduate measure, and the average taken as the value for the sample. The range in weight per bushel for the graduate measure was from 60.5 to 68.5 and for the pint measure from 59.0 to 67.0. The correlation coefficient between the weights obtained by these two methods was $\pm 0.947 \pm 0.005$. The 4.1 C.C. graduate measure and the pint weight per bushel measure are shown in figure 10.

FIGURE 10.

The pint weight per bushel measure and the 4.1 C.C.

graduate measure.

In order to judge the abilities of the various hybrids lines to produce plump grain under drought conditions, an estimate was made of the degree of shrivelling by assigning values of from 1 to 10, 1 being completely shrivelled and 10 completely plump.

The values obtained by the different methods were correlated with each other for the F_2 population 457 having in the F_3 a population of 225 plants. The data obtained is shown in table (43).

TABLE 43.

Correlation coefficients between the different methods of measuring the degree of shrivelling for the F_2 population 457 of I-28-60 x Milturum, grown at Brooks in 1932.

Methods correlated	Correlation coefficient
Weight 1000 kernels and weight 4.1 C.C.	+0.360±0.033
" 1000 " " plumpness index	+0.478±0.034
" " 4.1 C.C. and plumpness index	+0.872±0.011

The data in table (43) show that the weight per 1000 kernels was not as good an index as the other methods, probably due to the great variation in kernel size of the hybrid plants. The plumpness index appears to give a reliable index of the degree of shrivelling. This method owing to its rapidity of determination was used for the most part in this investigation.

TABLE 44

Mean and standard deviation of I-28-60 x Milturum F_3 lines, originating from separate F_2 populations, for plumpness index, grown at Brooks in 1932.

Parent or F_2 Population	Number of plants	Mean	S.D.
Milturum	82	7.11 $\pm$ 0.06	0.77 $\pm$ 0.04
I-28-60	85	4.16 $\pm$ 0.07	1.00 $\pm$ 0.05
455	388	5.95 $\pm$ 0.05	1.54 $\pm$ 0.04
456	322	6.12 $\pm$ 0.05	1.45 $\pm$ 0.04
457	315	5.88 $\pm$ 0.05	1.28 $\pm$ 0.03
458	311	5.99 $\pm$ 0.05	1.30 $\pm$ 0.04
460	852	5.79 $\pm$ 0.03	1.49 $\pm$ 0.02
461	173	6.31 $\pm$ 0.07	1.34 $\pm$ 0.05
462	313	4.76 $\pm$ 0.05	1.41 $\pm$ 0.04
463	288	5.97 $\pm$ 0.05	1.32 $\pm$ 0.04
464	131	5.73 $\pm$ 0.07	1.22 $\pm$ 0.05
467	235	5.02 $\pm$ 0.06	1.25 $\pm$ 0.04
469	222	5.59 $\pm$ 0.07	1.56 $\pm$ 0.05
471	332	5.36 $\pm$ 0.06	1.50 $\pm$ 0.04
472	280	6.20 $\pm$ 0.06	1.40 $\pm$ 0.04
473	410	6.38 $\pm$ 0.04	1.29 $\pm$ 0.03
474	358	5.53 $\pm$ 0.04	1.25 $\pm$ 0.03
Average	4930	5.78 $\pm$ 0.01	1.43 $\pm$ 0.01

The data in table (44) give the mean and standard deviation for the different F_2 populations and the parents of I-28-60 x Milturum grown at Brooks in 1932. Considerable variation is shown in the means of the different F_2 populations. The difference between the mean of any F_2 population and the one closest to it is not significant in any instance. There is a gradual gradation from the low mean of 4.76 ± 0.05 of F_2 population 462, to the high mean of 6.38 ± 0.04 of the F_2 population 473. This is a difference of 1.62 ± 0.07 , which is very significant. It is impossible to separate different F_2 populations into a number of distinct groups. These data suggest that there must be a large number of polymeric factors affecting the plumpness of kernel. The average plumpness of the F_2 populations is intermediate between the parents with a tendency towards the mean of the higher parent.

TABLE 45

The probable error and odds for the difference between the mean and standard deviation for plumpness index, of the average for the parental lines, and the F_3 lines originating from separate F_2 populations, of I-28-60 x Milturum, grown at Brooks in 1932.

F_2 pops.	Standard Deviation Comparison with				Mean Comparison with			
	I-28-60		Milturum		I-28-60		Milturum	
	P.E. Diff.	Diff. Odds	P.E. Diff.	Diff. Odds	P.E. Diff.	Diff. Odds	P.E. Diff.	Diff. Odds
455	.54+.06	8.4 V.G.	.77+.05	14.1 V.G.	1.79+.09	19.8 V.G.	1.15+.08	14.7 V.G.
456	.45+.06	6.9 V.G.	.68+.06	12.2 V.G.	1.06+.09	21.4 V.G.	0.98+.08	12.3 V.G.
457	.28+.06	4.5 416:1	.51+.05	9.6 V.G.	1.72+.09	19.4 V.G.	1.22+.08	16.2 V.G.
458	.30+.06	4.8 825:1	.53+.05	10.0 V.G.	1.83+.09	20.6 V.G.	1.11+.08	14.6 V.G.
460	.49+.06	8.5 V.G.	.72+.05	15.4 V.G.	1.63+.08	20.1 V.G.	1.31+.07	19.5 V.G.
461	.34+.07	4.8 825:1	.57+.06	9.0 V.G.	2.15+.09	24.0 V.G.	0.79+.08	10.3 V.G.
462	.41+.06	6.4 V.G.	.64+.05	11.7 V.G.	0.60+.09	6.6 V.G.	2.34+.08	29.7 V.G.
463	.32+.06	5.0 1350:1	.55+.05	10.0 V.G.	1.81+.09	20.8 V.G.	1.13+.07	15.2 V.G.
464	.22+.07	3.0 22:1	.45+.06	6.9 V.G.	1.54+.09	17.5 V.G.	1.37+.08	17.7 V.G.
467	.25+.06	3.9 116:1	.48+.06	8.6 V.G.	0.86+.09	9.4 V.G.	2.08+.08	25.6 V.G.
469	.56+.07	7.8 V.G.	.79+.06	12.2 V.G.	1.43+.09	15.9 V.G.	1.51+.08	19.5 V.G.
471	.50+.06	7.17 V.G.	.73+.06	13.1 V.G.	1.21+.08	6.9 V.G.	1.74+.08	23.0 V.G.
472	.40+.07	6.1 V.G.	.63+.06	11.1 V.G.	2.04+.08	24.5 V.G.	0.90+.08	11.6 V.G.
473	.29+.06	4.8 825:1	.52+.05	10.4 V.G.	2.22+.09	25.6 V.G.	0.72+.07	9.8 V.G.
474	.25+.06	4.1 175:1	.48+.05	9.4 V.G.	1.17+.09	13.5 V.G.	1.77+.07	24.1 V.G.

The data in table (45) give a comparison of the difference of the mean and standard deviation of the different F_2 populations with the parents. In practically every case the variability as measured by the standard deviation is significantly greater than either parent. Also the mean of every F_2 population is intermediate in respect to the parents and is significantly different from either parent.

Table 46

Frequency distribution of I-28-60 x Milturum F₃ and parental plants for, plumpness index, grown at Brooks in 1932.

Parent or cross	Plumpness index										Mean	S.D.
	1	2	3	4	5	6	7	8	9	10		
I-28-60	4	18	28	30	5						4.16+0.07	1.00+0.05
Milturum				2	14	42	22	2			7.10+0.06	0.77+0.04
F ₃ plants	6	37	216	579	871	948	1189	531	29	1	5.78+0.01	1.43+0.01

The data in table 46 give the distribution of all the I-28-60 x Milturum F₃ and parental plants for plumpness index, for the material grown at Brooks in 1932. The difference between the two parents of 2.84+0.09 is very significant. The difference in the variability of the F₃ and I-28-60 the most variable parent, of 0.43+0.05 is very significant. A few plants occurred beyond the limits of both parents, but this is not enough to indicate transgressive segregation. The data in table 46 is presented in graphical form in figure 11.

FIGURE 11.

Curves showing the distribution of I-28-60 x Milturum F₃ and parental plants, for plumpness index, grown at Brooks in 1932.

The plumpness index is shown along the horizontal axis, while the per cent. of the population for each plumpness index class is presented along the vertical axis; two scales being used, the smaller for the parents.

The data indicate that plumpness is partially dominant and that several main, as well as many minor polymeric factors govern this character. It was impossible to substantiate this data in the F_4 as the material at Brooks was completely haled out during July 1933.

The plumpness index was also obtained on the F_3 material grown at Fallis and Edmonton. An average plumpness index for each F_3 line was calculated for the material grown at the three places. These indices were correlated with each other and the data obtained is presented in table 47.

TABLE 47

Simple product moment correlation coefficients between I-28-60 x Milturum F_3 ^{for} average plumpness indices at Brooks, Edmonton and Fallis, grown in 1932.

Stations correlated	Correlation coefficients
Brooks and Edmonton	+0.384±0.038
Brooks and Fallis	+0.139±0.031
Edmonton and Fallis	+0.107±0.041

The significance of the correlation between the plumpness index at Edmonton and Brooks is probably because Brooks received more rain than normal, and Edmonton received less. At Fallis normal conditions prevailed and very little difference was found between the lines for plumpness of kernel. At Edmonton in normal years little variation in kernel

 

plumpness occurs. This shows the necessity of growing the hybrid material in an environment where a differential reaction can be obtained.

The data indicate that plumpness of kernel is an inherited character, which is in agreement with the work of Hayes (30).

Kernel Texture

Literature review.

Biffen (2) working with crosses between a hard Polish wheat and a soft Rivet wheat obtained a 3:1 ratio for hard to soft texture of kernels in the F_2 . Later (3) in a cross between Rough Chaff (soft) and Fife (hard) he found the hard translucent endosperm of Fife to behave as a simple dominant over the soft opaque endosperm of Rough Chaff. Howard and Howard (36) observed a monogenic ratio from a cross of a soft and a hard translucent wheat, the F_1 being intermediate. Freeman (21) made reciprocal crosses between a white Macaroni wheat with both a soft red bread wheat and Sonora 35 a soft white wheat. The F_1 were intermediate, while in the F_2 a series of gradations for texture were found. He proposes that two-factor pairs govern this character, which are cumulative in nature. He states the hard texture of the Macaroni wheat is due to a high per cent. of gluten in proportion to starch.

Bryan and Pressley (5) crossed Turkey Red and Sonora and found the F_1 intermediate while the F_2 indicated a one factor

difference. Harrington (28) in a series of crosses concludes seed texture is due to several factor pairs. Hayes (30) from a Marquis x Preston cross obtained a correlation of $+0.407 \pm 0.059$ between the F_4 and F_5 showing that Kernel texture is inherited. He states that ~~soft~~ ^{the} starchy or "yellow berry" ^{condition} is due largely to environment.

Engledow and Hutchinson (16) made crosses between T. turgidum (soft) x T. Durum (hard) and in the F_1 obtained completely vitreous kernels indicating complete dominance of the durum endosperm. They suggest two-factor pairs which separately give a durum like endosperm and jointly a true durum endosperm.

Clark, Florell and Hooker (11) studied texture in Hard Federation (vitreous) x Propo (soft) wheat crosses. The F_2 and F_3 were classified into 5 classes for texture as judged by the outward appearance of the kernels. The F_2 segregation approached a normal curve with a preponderance of hard texture lines indicating partial dominance of vitreous texture. In the F_3 they obtained indication of transgressive segregation and also true breeding intermediate lines. They concluded that texture is strongly inherited and suggested that several factor pairs were involved.

Bryan and Presley (7) crossed Baart a vitreous wheat and Sonora 103 a soft wheat. The F_1 plants were as soft as Sonora 103, showing a dominance of soft texture. The F_2 , F_3 and F_4 showed segregation for this character indicating ^{ed} a single main factor pair with numerous modifying factors.

Experimental methods and results.

Texture was studied in the F_2 and F_3 of I-28-60 x Milturum. The F_2 were grown in 1931 at Edmonton, where a good differential for texture was obtained. In 1932 the texture was determined for the average of each F_3 line at Fallis and Edmonton; the Brooks material was classified on the plant basis as being either starchy or vitreous. At Fallis a good differential was obtained, while at Edmonton and Brooks little variation in texture occurred in the F_3 . The material was classified for kernel texture by assigning values of from 1 to 10; 1 being completely starchy and 10 completely vitreous. Milturum was characterized by a completely starchy endosperm, while I-28-60 showed considerable variation, ranging from 5-10 in texture index.

The distribution for texture of the different F_2 populations both in the F_2 and F_3 showed considerable variation. The average texture for each F_2 population was calculated from which it was found that there were three distinct groups.

TABLE 48

Average texture index and standard deviation for I-28-60 x Milturum three texture groups and parents; grown in the F_2 at Edmonton and in the F_3 at Fallis.

Parent of hybrid group	F_2 Edmonton		F_3 Fallis	
	Average texture	S.D.	average texture	S.D.
Starchy F_2 populations	4.64 $\pm$ 0.16	2.09 $\pm$ 0.11	3.89 $\pm$ 0.10	2.03 $\pm$ 0.07
Semi-vitreous F_2 populations	7.33 $\pm$ 0.15	1.91 $\pm$ 0.15	6.21 $\pm$ 0.12	2.22 $\pm$ 0.08
Vitreous F_2 populations	8.18 $\pm$ 0.08	1.27 $\pm$ 0.05	7.60 $\pm$ 0.08	1.47 $\pm$ 0.06
I-28-60			7.00 $\pm$ 0.80	3.95 $\pm$ 0.57
Milturum			1.00 $\pm$ 0.00	0.00 $\pm$ 0.00

The data in table 48 show that the average texture of the three texture groups both for the F_2 at Edmonton and the F_3 at Fallis is as expected. At Fallis the starchy condition of the endosperm is expressed to a much greater extent than when grown at Edmonton. Fortunately for this study, 1931 at Edmonton was a comparatively wet season, which condition brings out the starchy endosperm to a much greater extent than would have occurred in a dry season such as 1932.

TABLE 49

Significance of the difference in texture index of the three hybrid texture groups for the F_2 and F_3 of I-28-60 $\times$ Milturum.

Texture groups	F_2 Edmonton			F_3 Fallis		
	D.	D./P.E. Odds		D.	D./P.E. Odds	
Starchy and semi-vitreous	2.69 $\pm$ 0.22	12.2	V.G.	2.32 $\pm$ 0.16	14.5	V.G.
Starchy and vitreous	5.54 $\pm$ 0.18	19.7	V.G.	3.71 $\pm$ 0.13	28.5	V.G.
Semi-vitreous and vitreous	0.85 $\pm$ 0.17	5.0	V.G.	1.39 $\pm$ 0.15	9.3	V.G.

The data in table 49 show that the difference between these three groups is very significant in both the F_2 and F_3 .

Figures 12 and 13 show in graphical form the distribution of the 3 groups for texture in the F_2 and F_3 respectively. In both figures 12 and 13 the texture index is expressed along the horizontal axis while the per cent. of the population in each class is given along the vertical axis. In figure 13 two scales are used for per cent. population, the smaller being for the parents. In the F_2 a break occurred at class 6 while in the F_3 the break occurs at class 5. Taking these classes as arbitrary dividing points in both the F_2 and F_3 excellent fits to the expected ratios are obtained, in every case, with the exception of the F_3 of the semi-vitreous group. Here a fair fit to the theoretical 3:1 ratio is obtained. These data are shown in table 50.

FIGURE 12.

Curves showing the distribution of I-28-60 x Milturum F_2 plants for texture index, grown at Edmonton in 1932.

FIGURE 13.

Curves showing the distribution of I-28-60 x Milturum F_3 lines and parental rows, for texture index grown at Fallis in 1933.

TABLE 50

The breeding behavior of I-28-60 x Milturum F_2 plants and F_3 lines of the starchy, semi-vitreous and vitreous texture groups, for texture index, and comparison with the 3:1, 3:1 and 15:1 ratios respectively.

Generation and Texture groups	Class	o	c	Dev.	P.E.	D/P.E.	Odds
F_2 starchy	starchy	61	60	1	2.61	0.38	<1
	vitreous	19	20				
F_2 semi-vitreous	starchy	20	18.3	1.7	2.50	0.68	<1
	vitreous	53	54.7				
F_2 vitreous	starchy	7	7.9	0.9	1.83	0.49	<1
	vitreous	119	118.1				
F_3 starchy	starchy	146	145.5	0.5	4.07	0.12	<1
	vitreous	48	48.5				
F_3 semi-vitreous	starchy	53	42	11.0	3.79	2.90	18.8:1
	vitreous	115	126				
F_3 vitreous	starchy	12	9.4	2.6	2.01	1.29	1.6:1
	vitreous	139	141.6				

The data indicate that one or both of the parents are heterogeneous for kernel texture. To all outward appearances Milturum is homogeneous for starchy endosperm. In 1932 at Fallis I-28-60 had a range from 5 to 10 for texture index which indicates that it must be heterogeneous for texture. One very interesting aspect of this study is that in certain F_2 populations we have starchy texture dominant by one main factor pair and in others vitreous texture dominant by either one or two main factors pairs. In the F_3 at Brooks and Edmonton texture was not studied in particular detail. However it was noticed that invariably the

starchy texture groups showed a much higher per cent. of starchy plants at both Edmonton and Brooks than either the semi-vitreous or vitreous texture groups. A review of the literature showed that in some cases vitreous texture had been found dominant and in other cases starchy or soft texture was dominant. The only possible explanation for the behavior of the material in these crosses is that I-28-60 is heterogeneous. In the vitreous texture group there must be two main factor pairs governing texture and in the semi-vitreous group one main factor pair, and in both cases a dominance of vitreous texture. While in the starchy texture group, we have starchy texture dominant by a single pair of factors. The reason for the reversal of dominance must be due to a type of inhibitor which either inhibits the expression of a dominant factor pair for starchiness in the semi-vitreous and vitreous texture groups or inhibits a dominant factor or factor pairs for vitreousness in the starchy texture group. This inhibitor in the vitreous and semi-vitreous groups does not interfere with the action of the dominant factor, or factor pairs for vitreous texture, nor in the starchy texture group does it interfere with the dominant factor pair for starchy texture. The inheritance of kernel texture is also probably influenced by a number of minor polymeric factors as well as the main factor pairs indicated above. Correlations coefficients were calculated between the behavior of the three texture groups, in the F_2 at Edmonton and the F_3 at Fallis, and also between the F_3 texture at Fallis and Edmonton. These data are shown in table 51.

TABLE 51

Simple product moment correlation coefficients between I-28-60 x Milturum, for the texture index of the three texture groups, grown in the F_2 at Edmonton and in the F_3 at Fallis, and between the F_3 at Edmonton and Fallis.

Variables correlated		correlation coefficients.
Vitreous group	F_2 and F_3	$+0.404 \pm 0.051$
Semi-vitreous group	F_2 and F_3	$+0.706 \pm 0.043$
Starchy group	F_2 and F_3	$+0.885 \pm 0.016$
Edmonton and Fallis	F_3	$+0.183 \pm 0.105$

The high correlations between the F_2 and F_3 further indicate that texture is inherited. The nonsignificant correlation between the F_3 at Edmonton and Fallis can only be explained by the fact that during 1932 the Edmonton material experienced a dry season, which tends to mark differences in texture. This latter correlation clearly shows, how great the environment influences kernel texture and also the necessity of growing the material under an environment which will give a differential reaction.

No other instance has been noticed in the literature review on the inheritance of kernel texture, in which certain F_2 populations from crosses between the same parents indicate a partial dominance of starchy texture and others a partial dominance of the vitreous texture. Biffen (2), Engledow and Hutchinson (16) and Clark, Florell and Hooker (11) all report a partial dominance of vitreous texture, while Bryan and Pressley (7) found dominance of starchy texture.

Crude-Protein

Literature review.

Biffen (2) working with crosses between a Polish wheat with a high nitrogen content and a Rivet wheat low in nitrogen content, obtained segregation in the F_2 for this character. He states that high nitrogen content is associated with hard translucent texture.

Clark (10) in the F_4 of reciprocal crosses of Kota x Hard Federation obtained transgressive segregation for crude-protein beyond the upper extremes of both parents. Clark and Hooker (12) in reciprocal crosses of Marquis x Hard Federation found the F_2 and F_3 intermediate between the two parents no evidence of transgressive segregation being obtained. They state that crude-protein is inherited in intermediate degrees between the parents by means of multiple factors. Correlation between the F_2 and F_3 were not significant which shows that crude-protein is easily influenced by the environment.

Clark, Florell and Hooler (11) in a series of crosses between Bobs, Hard Federation and Propo found a tendency for low protein content to be dominant. No indication of transgressive segregation was obtained. Correlations between the F_2 and F_3 showed that crude-protein content was not correlated one year with another.

Clark and Quisenberry (13) with Marquis x Kota found the F_2 and F_3 intermediate between and more variable than either parent. Several F_3 strains had lower crude-protein content than Marquis the lowest parent, indicating transgressive segregation.

Between the F_2 and F_3 high significant correlations were obtained.

Methods and experimental results.

The crude protein was determined by the (N. X 5.7 basis with 13.5% moisture), on 42 F_3 lines grown at Brooks and Edmonton and 132 F_3 lines grown at Fallis of I-28-60 x Milturum.

The data in table 52 show that the variability of the F_3 lines at all three stations is significantly greater than I-28-60 and about equal to that of Milturum. The difference between I-28-60 and Milturum of 2.06 ± 0.35 at Fallis and 2.7 ± 0.29 at Edmonton are significant. At Brooks however the both parents have an average crude-protein content of 16.15 per cent. At Fallis the F_3 showed considerable transgressive segregation, for crude-protein content less than Milturum, the lowest parent, no lines being obtained higher than I-28-60. While at Edmonton the low extreme of Milturum was not reached by any of the hybrids, five lines had a higher protein content than I-28-60. At Brooks four F_3 lines had a greater crude-protein content than either parent, none being below the lowest parent line. Low crude-protein content at Fallis showed partial dominance, while at Edmonton and Brooks a reversal of this occurred. This clearly showed that crude-protein content was very readily influenced by environmental conditions.

FIGURE 14.

Curves showing the distribution of I-28-60 x Miltutum F_3 lines and parental rows, for crude-protein content, grown at Fallis in 1933.

In figure 14 is given in graphical form the distribution of the F_3 hybrid lines and parental rows at Fallis for crude-protein content. Crude-protein content is presented along the horizontal axis while the per cent. of the population is shown along the vertical axis; two scales being used for per cent. of population, the smaller for the parents. An approximation to a normal curve was obtained which was similar to the distribution at Brooks and Edmonton. The distribution indicated a number of polymeric factors governing the inheritance of crude-protein content.

The data in table 53 give the correlation coefficients for crude-protein content between the F_3 lines grown at Edmonton, Brooks and Fallis.

TABLE 53

Simple product moment correlation coefficients
between I-28-60 x Milturum F_3 lines grown at
Edmonton, Fallis and Brooks during 1932.

Variables correlated	Correlation coefficients
Edmonton and Fallis	+0.509 <u>+0.077</u>
Edmonton and Brooks	+0.289 <u>+0.095</u>
Brooks and Fallis	<u>-0.160</u> +0.101

The correlation between Edmonton and Fallis is very significant, however between Edmonton and Brooks, and Brooks and Fallis the correlations are not significant. The polymeric factor hypothesis for the inheritance of crude-protein content is in agreement with that given by Clark and Hooker (12). The low

or nonsignificant correlations between crude-protein content of the hybrids grown at Edmonton, Fallis and Brooks; and that at Fallis there was a higher proportion of low protein lines, while at Edmonton and Brooks there was a higher proportion of high protein lines; indicate that this character is easily influenced by environmental conditions. This is in agreement with the data reported by Clark and Hooker (12) and Clark, Florell and Hooker (11). The occurrence of transgressive segregation agrees with the results of Clark (10) and Clark and Quisenberry (13).

RELATIONSHIP STUDIES BETWEEN THE CHARACTERS

General.

It is very important, in a plant breeding study, to have a knowledge of the relationships between the various characters. Selection maybe greatly facilitated, if it is shown that a ready classifiable character like glume color is linked with a physiologic character, like crude-protein content or yield. Such studies also indicate the extent to which the various desirable characters of each parent are associated with each other and the possibilities of obtaining in the hybrids suitable recombinations. In order to study statistically the possible relationships of the characters, they were divided into two main groups according to the nature of their inheritance. The first group, included the characters

of glume color and pubescence, awns, spike regularity, straw color and seed color, the inheritance of which is not influenced greatly by environment. In the second group were included the characters of strength of straw, height of plant, date of heading, grain yield, and plumpness, texture and crude-protein content of the kernels, the inheritance of which characters is readily influenced by the environment.

Tests of Independence or Association

The method used in measuring the independence or association of the characters in the first group, with each other and with the characters of the second group, was by contingency tables in which two characters are compared. The relationship between the distribution of the two characters was obtained by calculating χ^2 and determining the P value from Fisher's tables (17). In determining P from the tables, Fisher's suggestion for degrees of freedom was used. For example a 4 x 3 fold table has 6 degrees of freedom. A P value of .05 or less is necessary before it can be concluded that an association exists. A P value of .05 means that any association that exists between the distribution of the two characters might occur by chance in one out of twenty cases.

Literature reviews.

Influence of awns on yield.

Hayes (30), with Marquis x Preston reported that the bearded families averaged somewhat higher than the awnless families for yield. Clark (9) with reciprocal crosses of Kota x Hard Federation found the awned lines to outyield the awnless by 11 to 18 per cent. Clark, Florell and Hooker (11) in the crosses of Bobs x Propo and Hard Federation x Propo found a tendency for yield/increase^{to} with awn length.

Moskalenko (42) studied the dependence between awnedness and the elements of productivity for winter wheat hybrids. He concluded that during the years 1922, 1925, 1926 and 1927 there was no genetic relationship between awnedness and the elements of productivity under the conditions of the Ukranian steppe.

Clark and Quisenberry (13) in Kota x Marquis crosses grown at Bozeman, Montana found the opposite to previous reports, namely that the awnletted plants yielded significantly higher than the awned plants. Clark and Quisenberry and Powers (14) working with Hope x Hard Federation crosses found no relationship existing between awnedness and grain yield.

Influence of Awns on lodging.

Clark, Florell and Hooker (11) with crosses between Bobs and Hard Federation with Propo, report that lodging is associated with increase in length of awn. No other instances have been found in the literature between the characters studied in this investigation.

Experimental results.

In the crosses of I-28-60 x Milturum ^{glume}~~sheff~~ color was compared by Fisher's test of independence or association to see if there was any linkage relationships between this character and the characters of crude-protein content, texture and plumpness of kernel.

TABLE 54

Test of independence or association for I-28-60 x Milturum F₃ lines for glume color with crude-protein per cent. and texture index at Fallis, and plumpness index at Brooks.

Variables compared								X ²	P. value
Glume	color	seg.	3:1	and	protein	%	at Fallis	18.34	0.57
"	"	"	15:1	"	"	"	"	17.99	0.65
"	"	"	15:1	"	texture of starchy		group at Fallis	29.16	0.22
"	"	"	3:1	"	texture of semi-		vitreous group at Fallis	9.78	0.87
"	"	"	3:1	"	texture of vitreous		group at Fallis	9.20	0.82
"	"	"	3:1	"	plumpness at Brooks			7.24	0.51
"	"	"	15:1	"	"	"	"	15.74	0.41

The data in table 54 show that glume color in this cross is not linked in any way with crude-protein, texture and plumpness of the kernels.

Milturum had a narrow leaf and a more prostrate early

growth habit than I-28-60. An average figure for each of these two characters was obtained for each F_3 line grown at Brooks, on the basis of 1 representing narrow leaf width and prostrate growth habit and 5, wide leaf width and upright growth habit. The indices obtained were compared with the plumpness index at Brooks for the F_3 lines. A χ^2 of 24.18 with a P value of 0.23 was obtained between growth habit and plumpness index which indicates no association between growth habit and plumpness index; while a χ^2 of 34.93 with a P value of 0.02 was obtained between leaf width and plumpness index, which shows a significant association between these two characters.

Tests of association and independence were calculated for the characters in the first group with each other, and with the characters in the second group, for the crosses of Caesium with Marquis and Reward.

TABLE 55

Tests of independence or association for the Caesium x Marquis F_3 lines for the characters in the first group with the characters in the second group, grown in Edmonton in 1933.

	Lodging index		Height of plant		Date of heading	
	χ^2	P value	χ^2	P. value	χ^2	P. value
Spike regularity	28.70	0.16	26.98	0.14	35.72	0.03
Straw color	16.58	0.78	43.62	<0.01	80.18	<0.01
Awns	23.68	0.57	40.64	<0.01	24.62	0.32
Glume color	41.68	0.15	22.46	0.83	31.18	0.56

The data in table 55 show that straw color is strongly associated with both height of plant and date of heading in days; awns with height of plant; and spike regularity with date of heading. The white strawed F_3 lines are 36.60 ± 0.54 shorter than the purple strawed F_3 lines; while the white strawed F_3 are 2.45 ± 0.20 earlier than the purple strawed F_3 lines. Since only one pair of ~~fact~~ factors governs straw color in these crosses, the factor pair for straw color/^{must}reside on the same homologous chromosomes as one of the factor pairs governing both date of heading and plant height. This is also supported by the fact that heading and height are also strongly correlated with each other.

The awnletted F_3 lines of the reciprocal crosses of Caesium x Marquis are 1.95 ± 0.53 cms. taller than the awned F_3 lines. This would necessitate that Marquis, the short parent, having a dominant factor for tallness which is situated on the same chromosomes as the gene governing awn expression. In the distribution of the F_3 lines several lines are slightly taller than the tallest Caesium parent while several lines are shorter than the shortest Marquis parent. This slight transgressive segregation is also indicative that Marquis possesses a factor pair for tallness.

The regular spike F_3 lines are 0.71 ± 0.23 days earlier than the irregular spike F_3 lines. This indicates that the factor pair for spike regularity and one of the ^{pairs for} factors/date of heading in this cross are located on the same homologous chromosomes. No association is indicated between the other characters presented in table 55.

TABLE 56

Test of independence or association for
Caesium x Marquis F_3 lines, for the
characters in the first group with each
other grown at Edmonton in 1933.

Characters compared	χ^2	P. value
Awns and glume color	7.91	0.00
Awns and spike regularity	2.73	0.61
Awns and straw color	4.94	0.29
Spike regularity and straw color	0.99	0.91
Spike regularity and glume color	8.33	0.22
Straw color and glume color	5.64	0.49

The data in table 56 show that these characters are inherited independently of each other. Since both straw color and awns are linked with height of plants and are not with one another, it indicates that height of plant is governed by at least two-factor pairs. Similarly since both spike regularity and straw color are linked with date of heading but not with each other, date of heading is also governed by at least two-factor pairs.

TABLE 57

Tests of independence of association for
Reward x Caesium F₃ lines for the characters
in the first group with the characters in the
second group, grown at Edmonton in 1933.

	Lodging index		Height of plant		Date of heading		Grain yield	
	X ²	P. value	X ²	P. value	X ²	P. value	X ²	P. value
Glume pubescence	8.50	0.97	22.55	0.32	23.02	0.29	17.02	0.52
Straw color	20.01	0.34	25.25	0.19	22.65	0.27	24.53	0.15
Awns	17.30	0.50	33.14	0.035	14.80	0.79	17.20	0.50
Glume color	24.31	0.61	24.89	0.73	28.39	0.55	19.36	0.85

The data in table 57 show that all the characters are inherited independently save awns which is associated with height of plants. The awned plants as in the reciprocal crosses of Caesium x Marquis are shorter than the awnless plants. This indicates that the Reward parent has a gene for tallness located on the same chromosome as the gene for the awnletted condition. The fact that white straw color is not significantly associated with height of plants and date of heading in Reward x Caesium suggests that the constitution of Marquis and Reward is not the same for the factors governing height and heading.

TABLE 58

Tests of independence of association for
Reward x Caesium F₃ lines for the characters
in the first group with each other, grown at
Edmonton in 1933.

Characters compared	χ^2	P. value
Awns and glume color	10.46	0.14
Awns and glume pubescence	7.28	0.13
Awns and straw color	5.53	0.24
Glume pubescence and straw color	4.63	0.33
Glume pubescence and glume color	3.63	0.73
Straw color and glume color	4.71	0.58

The data in table 58 show that the above four characters are inherited independently.

In the crosses of Caesium with Reward and Marquis no association was found between awns and yield which agrees with the findings of Moskalenko (42) and Clark, Quisenberry and Powers (14). Other investigators cited found a tendency for yield to increase with awn length with the exception of Clark and Quisenberry (13) who report the awnletted plants yielded significantly higher than the awned plants.

No association was found between awns and lodging which is not in agreement with the results of Clark, Florell and Hooker (11) who report that lodging is associated with an increase in the length of the awn.

CORRELATION STUDIES

Plumpness and yield

Literature review.

Hayes (30) with Marquis x Preston reports positive correlations between yield and plumpness. Hayes, Aamodt and Stevenson (32) found in rod row trials of spring and winter wheat high positive correlations between yield and plumpness. Bridgford and Hayes (4) grew 61 strains of hard red spring wheat at Morris Minn. They found high positive correlations between yield, correlated with plumpness and weight per 1000 kernels, the former correlation being the more significant. Smith and Clark (49) report very significant positive correlations between Kernel plumpness and yield and weight per 1000 kernels in durum crosses between Pentad and Nodak crossed with Akrona.

Waldron (69) grew 25 varieties of wheat hybrids under conditions of high temperature and low moisture at Fargo N.D. in 1932. He correlated yield, weight per bushel, weight per 1000 kernels and plumpness, in all possible combinations. In all cases he found significant positive correlations. Yield was more highly correlated with weight per 1000 kernels, than with plumpness, which was next and least with weight per bushel. Plumpness was correlated to approximately the same degree with both weight per bushel and weight per 1000 kernels. The correlation between weight per bushel and weight per 1000 kernels was significant but not as large as the other correlations.

Experimental methods and results.

The F_2 population 457 of I-28-60 x Milturum grown under drought conditions at Brooks in the F_3 was studied on the individual plant basis for yield, weight per bushel, weight per 1000 kernels and plumpness index. The methods used have been described previously under plumpness studies.

TABLE 59

Simple product moment correlation coefficients for I-28-60 x Milturum F_2 populations 457 between yield, weight per bushel, weight per 1000 kernels and plumpness index, grown in the F_3 at Brooks in 1932.

Variables correlated	correlation coefficient
yield and plumpness	+0.148 $\pm$ 0.040
yield and weight per bushel	+0.081 $\pm$ 0.044
yield and weight per 1000 kernels	+0.315 $\pm$ 0.034
plumpness and weight per bushel	+0.872 $\pm$ 0.011
plumpness and weight per 1000 kernels	+0.478 $\pm$ 0.034
weight per bushel and weight per 1000 kernels.	+0.360 $\pm$ 0.039

The data in table 59 show that in this F_2 population yield was more dependent on weight per 1000 kernels than the plumpness index, and was not significantly related to weight per bushel. This may be partially explained owing to the great variation in the size of the kernels of the hybrid plants. Plumpness of kernel was much closer associated with weight per bushel than it was with weight per 1000 kernels, this again is

partially due to kernel size. The correlation between weight per bushel and weight per 1000 kernels was significantly lower than the two previous correlations.

The correlation between yield and weight per 1000 kernels was much more significant than that between yield and plumpness index, which is in agreement with the results of

Waldron (69). The data of other investigators (4, 30, 32, 49, 69) cited in the literature review found that the correlation between kernel plumpness and yield was very significant, however in the present study the correlation between these two characters was barely significant.

Plumpness and date of heading

Literature review.

Smith and Clark (49) in durum crosses between Pentad and Nodak with Akrona report the relation between heading and plumpness to be indefinite. Hayes, Aamodt and Stevenson (32) in rod row trials of spring and winter wheat at Waseca in 1926 found no correlation between plumpness and heading of the spring wheats, however with the winter wheats they obtained a significant negative correlation. Bridgford and Hayes (4) correlating plumpness and heading in 61 strains of spring wheat grown at Morris Minn. in a variable season, report a positive correlation of 0.45 ± 0.07 . Waldron (69) reports on 25 hybrid varieties of spring wheat grown at Fargo N.D. in 1932, under conditions of high temperature and low moisture, a significant negative correlation between plumpness and heading.

Methods and experimental results.

In the present study the heading of the F_3 rows of I-28-60 x Milturum grown at Brooks was estimated when 50 per cent. of the plants were headed. This was found to be correlated with plumpness to the extent of $+0.268 \pm 0.03$. Milturum was late and plump while I-28-60 was early and shrivelled.

The significant positive correlation obtained between kernel plumpness and heading is in agreement with the work of Bridgford and Hayes (4). Waldron (69) and Hayes, Aamodt, and Stevenson (32), the latter with winter wheat, report significant negative correlations, while Smith and Clark (49) and Hayes et al (32) with spring wheat found no relationship between these two characters. These results indicate that the association between plumpness of kernel and heading is dependent both on the material used and the environment under which the material is grown.

Plumpness with crude-protein and texture.

Literature review.

Bailey and Hendel (1) studying the 1911, 1912, 1913 and 1921 wheat crops of Minnesota report no correlation between wheat kernel plumpness and crude-protein content, when the former was measured in terms of either weight per 1000 kernels or weight per bushel. Waldron (69) in rod row trials of spring wheat hybrids found per cent. crude-protein to be negatively associated with weight per bushel, weight per 1000 kernels and plumpness. While the per cent. yellow berry was

positively associated with these characters. This shows that the plump samples have a lower crude-protein content and a greater per cent. of yellow berry than the shrivelled samples. Smith and Clark (49) found no significant correlation between kernel plumpness and protein content in crosses of Pentad and Nodak with Akrona.

Experimental results.

TABLE 60

Simple product moment correlation coefficients for I-28-60 x Milturum F₃ lines, between plumpness index compare with crude-protein per cent. and texture index.

Variables correlated	Correlation coefficient
Plumpness, Brooks and Protein Brooks	$-.056 \pm 0.104$
Plumpness, Brooks and protein, Fallis	$+0.014 \pm 0.059$
Plumpness, Edmonton and protein Edmonton	$+0.119 \pm 0.103$
Plumpness, Edmonton and protein Fallis	$+0.030 \pm 0.063$
Plumpness, Fallis and protein Fallis	$+0.000 \pm 0.000$
Plumpness, Brooks and Texture , Fallis (starchy group)	$+0.061 \pm 0.052$
Plumpness, Brooks and texture Fallis (semi-vit. group)	$+0.061 \pm 0.055$
Plumpness, Brooks and texture, Fallis (vitreous group)	$+0.151 \pm 0.057$
Plumpness, Edmonton and texture, Edmonton	$+0.133 \pm 0.102$

In no case are the correlations presented in table 60 significant, which shows that with this cross and under the conditions which the material was grown plumpness index was not associated with either crude-protein per cent. or texture index.

This lack of association of plumpness index with either crude-protein content of kernel texture is in agreement with the results of Bailey and Hendel (1) and Smith and Clark (49) but however disagrees with the results of Waldron (69).

Texture and crude-protein content.

Literature review.

Clark (10), with Hard Federation x Propo crosses grown at Davis California, found a high positive correlation between texture and crude-protein per cent. in the F_3 . However he states that high protein content is not necessarily associated with hard texture, which is indicated by both the lack of significant correlations between the F_2 and the F_3 for protein per cent. and the partial dominance of low protein and vitreous texture individuals in the F_2 . Clark, Florell and Hooker (11), in crosses between Bobs, Hard Federation and Propo wheats, report that there is a slight tendency toward increased protein content with the increase in hardness of the kernel texture. Hayes, Immer and Bailey (34) studied the relationship between protein and texture of diverse hybrid strains of spring and winter wheats grown at four points in Minn. for the years 1924 to 1926. They found no indication that protein content and

texture are positively correlated. Waldron (69) in 1932 grew 25 hybrid varieties of spring wheat and report the high negative correlation of -0.706 between per cent. crude-protein and per cent. yellow berry.

Experimental results.

TABLE 61

Simple product moment correlation coefficients
for I-28-60 x Milturum F_3 lines between texture
index and crude-protein per cent.

Variables correlated	Correlation coefficients
Texture and protein, vitreous texture group at Fallis	$+0.668 \pm 0.068$
Texture and protein, semi-vitreous texture group at Fallis.	$+0.473 \pm 0.084$
Texture and protein, starchy group at Fallis	$+0.551 \pm 0.060$
Texture and protein, total population at Fallis	$+0.503 \pm 0.043$
Texture and protein, total population at Edmonton	$\pm 0.027 \pm 0.104$

The data in table 61 show that at Fallis protein is strongly associated with texture but such is not the case at Edmonton.

In the discussion under the inheritance of texture it was shown that there were three distinct groups of F_2 populations in regard to the inheritance of this character. It was thought that since texture at Fallis was so strongly correlated with crude-protein

that there would be a wide difference in the average crude-protein content of the three texture groups. This was not found to be the case. The average per cent. crude-protein was 12.16 ± 0.12 , 12.49 ± 0.15 and 12.65 ± 0.18 for the starchy, semi-vitreous and vitreous texture groups respectively. These differences are not significant. The reason for this apparent paradox is shown by the data in table 62.

TABLE 62

Relationships existing for I-28-60 x Milturum
F₃ lines between texture and crude-protein per
cent. in the three texture groups grown at
Fallis in 1932.

Starchy texture group		Semi-vitreous texture group		Vitreous texture group	
Texture range	Av. % protein	Texture range	Av. % protein	Texture range	Av. % protein
1-5	11.9	1-5	11.8	1-5	11.0
6-10	13.3	6-10	12.9	6-10	13.0
Av. 1-10	12.18	1-10	12.49	1-10	12.65

The data in table 62 show that the starchy texture lines of the starchy texture group had a higher per cent. crude-protein than the starchy texture lines of the vitreous texture group, the same relationship also held for the vitreous texture lines of each group. This difference was sufficient to balance the expected

 

significant differences between the three groups for average crude-protein per cent. The data indicate that some of the factors governing crude-protein content and the texture of the grain are linked, while others are inherited independently.

In the literature review is shown that considerable differences of opinion exists as to the relationship between kernel texture and crude-protein content. In this investigation at Fallis very significant correlations between kernel texture and crude-protein content were obtained, while at Edmonton the correlation was non-significant. These data and those of other investigators indicate that the relationship between these two characters is greatly influenced by environment.

Literature reviews.

Grain yield and date of heading.

Clark (9), using Kota x Hard Federation correlating yield and heading in the F_2 and F_3 , found the early plants more productive. Goulden and Elders (26), in rod row trials of 146 varieties of spring wheat at Winnipeg in 1925, found that earliness was positively correlated with yield. This, they explained was partially due to fact that a rust epidemic came late in the season, the earlier varieties thus escaping damage. Clark and Hooker (12), with reciprocal crosses of Marquis x Hard Federation found heading not to be correlated with yield, however they found the fruiting period positively correlated with yield. Hayes, Aamodt and Stevenson (32), with rod rows trials found a negative correlation between heading and yield but it was not significant. Bridgford and Hayes (4), in rod row trials of 61 strains of spring wheat at Morris Minn. found a

low significant positive correlation between heading and yield. Smith and Clark (49), in crosses between Pentad and Nodak with Akrona, found yield negatively associated with heading. Waldron (69), reports a very significant negative correlation between yield and heading for 25 hybrid varieties of spring wheat. He states that evidently a lengthened period of photosynthetic activity normally considered desirable for good yields may be more than offset by injurious seasonal conditions of low moisture.

Grain yield and height of plant.

Clark (9) in the F_2 and F_3 of Kota x Hard Federation crosses, found significant positive correlations between yield and height. Clark and Hooker (12) in the F_2 and F_3 of Marquis x Hard Federation found a high positive correlation between height and yield. Hayes, Aamodt and Stevenson (32) in rod row trials of spring and winter wheat report positive correlations between height and yield. Bridgford and Hayes (4), in rod row trials of 61 strains of spring wheat at Morris Minn. obtained significant positive correlations between height and yield. Waldron (69), found no correlation between height and yield, with 75 varieties of spring wheat hybrids, grown at Fargo N.D. in 1932.

Grain yield and lodging.

Goulden and Elders (26), in rod row trials of 146 spring wheat varieties, found the weak strawed varieties to yield the highest.

Date of heading and height of plants.

Clark (9) in reciprocal crosses between Kota x Hard Federation found a negative but not significant correlation between heading and height under favorable conditions at Davis, California. However under unfavorable conditions due to drought and rust at St. Paul Minn. and Mandan, N.D., he obtained significant positive correlations between these two characters. Clark and Hooker (12) with reciprocal crosses of Marquis x Hard Federation, found that the correlations between heading and height was not significant but that the correlation between ripening and height was significant. Hayes, Aamodt and Stevenson (32), with rod row tests of spring and winter wheat varieties, report positive correlations between height and heading. Bridgford and Hayes (4), with 61 strains of wheat grown in rod rows, however found a significant correlation between these characters.

Date of heading and lodging.

Goulden and Elders (26), in rod row trials with 146 strains of spring wheat grown at the Dominion Rust Laboratory, Winnipeg, in 1925, report a positive but nonsignificant correlation between straw strength and ^{date of} heading.

Experimental results.

Simple and partial correlations were run between heading, height, lodging and yield of the F_3 lines of the crosses of Caesium with Marquis and Reward grown at Edmonton in 1933.

TABLE 63

Simple product moment and first order partial correlation coefficients for Reward x Caesium F_3 lines, between date of heading, plant height, lodging index and grain yield, grown at Edmonton in 1933.

Variables correlated	Simple product moment corr. coefficients	First order partial corr. coefficients
Yield and heading	+0.101 <u>+0.088</u>	
Yield and height	+0.162 <u>+0.087</u>	
Yield and lodging	+0.054 <u>+0.089</u>	
Heading and height	+0.284 <u>+0.054</u>	+0.290 <u>+0.054</u>
Heading and lodging	+0.191 <u>+0.057</u>	+0.161 <u>+0.057</u>
Height and lodging	+0.252 <u>+0.057</u>	+0.253 <u>+0.055</u>

The data in table 63 show that yield is not related to any of the other three variables, by the simple product moment coefficients, hence it was not used in calculating the partial correlations.

TABLE 64

Simple product moment and first order partial correlations coefficients for Caesium x Marquis F_3 lines, between date of heading, lodging index and plant height, grown at Edmonton in 1933.

Variables correlated	Simple product moment Corr. coefficients	First order partial Corr. coefficients
Heading and height	+0.379 <u>+0.034</u>	+0.416 <u>+0.032</u>
Heading and lodging	+0.216 <u>+0.017</u>	+0.171 <u>+0.018</u>
Height and lodging	+0.291 <u>+0.037</u>	+0.314 <u>+0.036</u>

The data in tables 63 and 64 show significant correlations between heading and height, heading and lodging, and height and lodging for both series of crosses. Height was correlated to a greater extent with heading than with lodging; and lodging to a greater extent with height than with heading. The partial correlations in both series of crosses increased the significance of the correlations between heading and height, and lodging and height at the expense of the heading and lodging correlation.

In the literature review on the relation between grain yield and date of heading both negative and positive correlations have been reported. This indicates that the relationships between these two characters is influenced greatly by the environment. The lack of correlation between these two characters in this investigation is in agreement with the results of Clark and Hooker (12).

In this study no correlation was found between plant height and grain yield which is in agreement with the results of Waldron (69) but is in disagreement with the results of the other investigations reviewed.

No correlation was found between lodging index and grain yield in this study which does not agree with the results of Goulden and Elders (26).

The positive correlations between date of heading and plant height in this investigation are in agreement with the results of Hayes, Aamodt and Stevenson (32) and those of Clark's at Davis.

In the present study small positive but significant correlations were found between date of heading and plant height

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which agrees with the tendency reported by Goulden and Elders (26).

ECONOMIC SIGNIFICANCE

It is as yet too early to state definitely if drought resistant lines of high quality will be obtained from the crosses studied. From I-28-60 x Milturum ^{F₃ lines,} plants were selected, ~~from~~ ^{F₃ lines,} the kernels of which possessed the plumpness of Milturum at Brooks, and the vitreous texture of I-28-60 at Fallis; these were grown in the F₄ during 1933. At Fallis a large percentage of the selected plants were homozygous for vitreous texture; while at Edmonton, a number of the vitreous texture Fallis lines, were homozygous for the strong straw and earliness of I-28-60. As previously stated the F₄ grown at Brooks was hailed out, as a result the inheritance of seed plumpness could not be substantiated. During 1934 in the F₅ 15 bulked lines apparently homozygous for texture, kernel size and shape, maturity, height and strength of straw, as well as several hundred promising plant selections will be tested at Brooks, Fallis and Edmonton.

The F₃ segregation in the crosses of Caesium with Reward and Marquis, clearly indicated that it is possible to obtain lines possessing the desirable characters of early maturity, strong straw and vitreous texture, Two bulked lines ^{and} over 1000 individual plant selections will be given a further test in the F₄.

SUMMARY

1. This genetic study was undertaken with the object of securing a high-yielding, strong-strawed, hard red spring wheat of superior quality and possessing a greater resistance to drought than the varieties grown at present.

2. The Milturum and Caesium parents were selected for their high yielding capacity and their ability to withstand drought better than the standard Canadian varieties.

3. The material was grown at three points; at Edmonton under ideal conditions, at Brooks under droughty conditions and at Fallis in the grey wooded soil area.

4. The crosses between I-28-60 x Milturum were studied in the F_2 and F_3 at Edmonton, Brooks and Fallis to determine the inheritance of, and relation between the following character pairs; brown vs. white glume color; plump vs. shrivelled kernel; vitreous vs. starchy kernel texture; and high vs. low crude-protein content. Crosses between Reward x Caesium and reciprocal crosses of Caesium x Marquis were studied in the F_2 and F_3 at Edmonton and Fallis to determine the inheritance of, and relation between the following character pairs; brown vs. white glume color; pubescent vs. glabrous glume; awnletted vs. awned; irregular vs. regular spike; purple vs. white straw color; red vs. white seed color; strong vs. weak straw; short vs. tall height of plant; early vs. late heading; and low vs. high grain yield. All characters of the first group and texture were studied in the F_2 and F_3 , while plumpness of kernel, protein

content, lodging index, plant height, date of heading and grain yield were studied only in the F_3 .

5. It was shown that Milturum was not homogeneous for glume color, for certain F_2 populations of I-28-60 x Milturum gave a two-factor differential while others only one, for this character. A two factor difference was found to explain the inheritance of glume color in the crosses of Caesium with Reward and Marquis. In all crosses white glume color was recessive.

6. Glume pubescence in Reward x Caesium was shown to be inherited in a monohybrid ratio, the pubescent condition being partially dominant.

7. The awnletted condition was found to be partially dominant over the awned condition by one main factor pair, in the crosses of Caesium with Reward and Marquis. An excess of awned plants, as well as many different intermediate awn types, suggests the presence of modifying factors.

8. Spike regularity was shown to be recessive to the irregular spike, by one-factor pair in Caesium x Marquis.

9. Purple straw was found partially dominant to white straw by a single gene, in the crosses of Caesium with Reward and Marquis.

10. A 63 red to 1 white ratio was obtained for seed color, which shows that Marquis and Reward have two factor pairs for red seed color, while the third pair is possessed by Caesium.

11. Lodging in the Caesium x Marquis was controlled by one main factor pair; while with Reward x Caesium two main

factor pairs were indicated. In both series of crosses minor modifying factor pairs are believed to modify the expression of this character. Strong straw, in both series of crosses was partially dominant. Transgressive segregation did not occur for this character.

12. Plant height, in the crosses of Caesium with Marquis and Reward, appeared to be controlled by polymeric factors. In Caesium x Marquis the mean was midway between the two parents, while in Reward x Caesium there was a partial dominance of tall straw. Slight transgressive segregation occurred in Reward x Caesium.

13. Date of heading, in the crosses of Caesium with Marquis and Reward, was indicated as being governed by polymeric factors, with a partial dominance of earliness. Transgressive segregation occurred in the crosses of Caesium x Marquis.

14. Grain yield in Reward x Caesium was indicated as being governed by polymeric factors, with a partial dominance of the low yield of Reward.

15. Plump kernel, in I-28-60 x Milturum was shown to be partially dominant to shrivelled kernel. This character appeared to be inherited by several main, as well as many minor factor pairs.

16. In the inheritance of kernel texture, in I-28-60 x Milturum, certain F_2 populations for both the F_2 and F_3 indicated a partial dominance of vitreous texture by two main factor pairs, others by one main factor pair; while in still a third group starchy texture was partially dominant by one main factor pair. Minor polymeric factors also probably influence the inheritance of this character.

17. Crude-protein inheritance, in I-28-60 x Milturum was indicated as being controlled by a number of polymeric factors. The lack of correlation, between the replicates grown at Brooks and Edmonton, and Brooks and Fallis, indicated that crude-protein is readily influenced by the environment. Transgressive segregation occurred at all three places.

18. Glume color, in I-28-60 x Milturum was found to be inherited independent of crude-protein, texture, and plumpness of the kernel.

19. In Caesium x Marquis grown at Edmonton, spike regularity was found to be linked with date of heading; straw color with both height of plant and date of heading; and awns with height of plant. While in Reward x Caesium awns were found associated with date of heading. No other cases of linkage were found between any of the other characters compared in the two series of crosses.

20. No relationship existed between awns and grain yield in Reward x Caesium grown at Edmonton.

21. In the F_3 of I-28-60 x Milturum grain yield was found to be more closely associated with weight per 1000 kernels than with plumpness index or weight per bushel. The correlation between plumpness index and weight per bushel was much more significant, than those between plumpness index and weight per bushel, with weight per 1000 kernels.

22. Plumpness index was found to be positively correlated with date of heading, at Brooks, for the F_3 of I-28-60 x Milturum.

23. Plumpness index was shown to be in no way associated with texture index or crude-protein in the F_3 I-28-60 x Milturum.

24. Texture index and crude-protein content, for the F_3 of I-28-60 x Milturum were strongly correlated with each other at Fallis; however at Edmonton no correlation was found between these two characters. There was not a significant difference between the average crude-protein of the three texture groups grown at Fallis; certain of the factor pairs governing crude-protein and kernel texture inheritance are apparently linked, while others are inherited independently.

25. The F_3 data of Reward x Caesium at Edmonton indicate that grain yield is inherited independent of date of heading, plant height and strength of straw.

26. Date of heading, plant height and lodging index were all positively correlated with one another, in the crosses of Caesium with Reward and Marquis. In order of significance the correlations were, date of heading and plant height; plant height and lodging index; and date of heading and lodging index.

27. Selections have been made from the more promising lines of all the crosses studied, both to further study the inheritance of a number of the more complex characters, and with the hopes of obtaining superior varieties. Strong strawed lines possessing plump kernels of good type and vitreous texture predominate among the selections.

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