THESIS

on

The Inheritance of Head Characters in A Species Hybrid of Wheat.

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INTRODUCTION

Explanation and Purpose

This thesis constitutes a report of work done by the writer in the study of the inheritance of head characters in a cross of Cornwheat X Marquis (Triticum polonicum X T. vulgare). It had its inception in the summer of 1922 when the writer was first employed in making wheat hybrids at the Washington Experiment Station. This work involved the making of a number of species crosses. The value of such hybrids in studying the relation of species to species was first suggested by reading "The Origin and Relationships of the Races of Wheat", in Percival's book, "The Wheat Plant". Further interest in species hybrids as a possible source of new and improved forms was aroused by conversations with Dr. E. F. Gaines, and by reading reports of cytological investigations in species crosses by Kihara (14) and by Sax (17). Later on work was undertaken in three crosses between Triticum vulgare and Aegilops cylindrica, and in one cross between T. vulgare and T. polonicun (Bluestem X Cornwheat). In 1924 the present study was begun by compiling data on parent material and on the F1 and F2 generation of the Cornwheat X Marquis cross. The following year the F3 generation was grown and the data compiled.

This cross is especially valuable for the study of inheritance in wheat for the following reasons; first, the parents have many contrasting characters; second, the species differ in chromosome number; third, the F1 plants produce a sufficient number of viable seeds to insure a fair sized F2 population.

There were three principal reasons for taking up this study. These were; first, to study the inheritance of the characters involved; second, to determine if possible if any of these characters were carried by the "vulgare set" of chromosomes; and third, to investigate all evidence which would throw any light on the origin of Triticum polonicum.

ACKNOWLEDGEMENTS

In presenting this thesis, I wish to express my appreciation to all those who have been of assistance in its preparation.

To Dr. E. F. Gaines, cerealist of the Washington Experiment Station, I am especially indebted for his generosity in furnishing the plant material for this study, and for his never-failing interest in the problem, as well as for his many valuable criticisms.

I wish to thank Professor G. R. Hyslop for furnishing the facilities for continuing the study of this cross at the Oregon Agricultural College, and Professor E. N. Bressman for constructive criticism and helpful suggestions.

Credit is also due the Farm Crops Department of the State College of Washington for assistance in compiling the data for the F2 and F3 generations, and to The Washington Experiment Station for space in the cereal nursery.

CONDITIONS AFFECTING THE WORK.

The study of the Cornwheat X Marquis cross was begun by the writer during the summer of 1924. The F2 generation, together with F1 plants from which data herein used were procured, was grown at the Washington Experiment Station in 1920. The parent material described was also grown there that year. At the time this work was undertaken, many of the heads of both the parent and hybrid material were more or less badly shattered, so could not be used for compiling data. Ten heads of Cornwheat and ten of the F1 hybrid were used to obtain fair average samples. Only five heads of Marquis were of such condition that they could be used. Data were taken from all the F2 heads that were in a sufficiently good condition to be used. These numbered 147 heads. Detailed data were secured from the parent and F1 heads on seven characters. Data on twelve characters were taken from the F2 plants.

All seeds from each head were saved and placed in a sealed envelope. In the spring of 1925, head rows were planted from all F2 heads that had produced ten or more seeds. The F3 generation was harvested during August 1925 and data taken from the same characters as in the F2 generation.

The work of arranging the data and the study of the inheritance of the various characters was done principally at the Oregon Agricultural College during the winter of 1925-26.

DESCRIPTION OF PARENTS.

Cornwheat and Marquis have many contrasting characters. Some of the outstanding differences are; length, texture and shape of glumes, awned condition, color of awns, and length, shape and color of seed. Cornwheat also has a pithy stem, while Marquis has the hollow stem characteristic of vulgare wheats. Cornwheat belongs to the species Triticum polonicum which has fourteen chromosomes in the haploid number. Marquis is a T. vulgare variety and has twenty-one haploid chromosomes. The United States Department of Agriculture Bulletin 1074 gives the following description of the two varieties:

White Polish (Cornwheat)

"Plant spring habit, early, tall; stem white, weak; spike awned, linear-oblong, lax, nodding; glumes glabrous, white, paperish, very long, narrow; shoulders usually wanting, beaks narrow, acute, 0.5 to 1 mm. long; awns black, usually deciduous, 4 to 10 cm. long; kernels white (amber) very long, hard, elliptical, acute; germ midsized, crease narrow, shallow to middeep; cheeks usually rounded; brush large, midlong."

Marquis.

"Plant spring habit, early, short to midtall; stem white, strong; spike awnless, fusiforn, dense, erect; glumes glabrous to yellowish, short, wide; shoulders midwide to wide, usually square; beaks wide, acute 0.5 mm. long;

apical awns few, 1 to 10 mm. long; kernels red, short, hard, ovate, with truncate tip; germ midsized; crease wide, deep; cheeks angular; brush midsized, midlong."

T. polonicum is not important commercially, but has many characters of interest to the plant breeder. Its origin is not definitely known. The earliest reference to it appears in the literature of the seventeenth century. It is thought to be of European origin. Percival (16) states that T. polonicum is probably a mutation of T. durum, or that it may be a race resulting from a cross of T. Durum with some other species. In this country it was grown in Maryland as early as 1845. Since then it has, from time to time, been exploited by unscrupulous seedsmen who have distributed it under the names of Giat Rye, German Rye Wheat, Goose Wheat, Wild Goose Wheat, and others. It has in this way, been introduced into many communities, but has never been gown for more than a year or two in any one place, excepting as a novelty. Yields are poor and there is no market for the grain, excepting for feed.

Marquis is the most important variety of hard red spring wheat grown in North America. It is of hybrid origin, the result of a cross between an early ripening Indian wheat known as Hard Red Calcutta and Red Fife, a common American variety of hard red spring wheat. The original cross was made by Dr. William Saunders of the

Dominion Department of Agriculture, Ottawa, Canada. Selections from the hybrid stock were made and tested by Dr. C. E. Saunders. Marquis was first grown in the pure state in 1904, but was not distributed until the completion of tests, lasting until 1907. Since then its culture has expanded rapidly until now the variety constitutes about sixty percent of the spring wheat grown in North America.

Table 1 gives the average values for seven characters in the Cornwheat parent. Table 2 shows the range and average for the corresponding characters in the Marquis parent.

Table 1.

Cornwheat parent.

Rachis Length	Awn Length	Glume Length	Lemma Length	No. of seeds	No. of Internodes	Seed Length
116	105	27	22	18	19.3	10

Table 2.

Marquis Parent.

Rachis Length	Awn Length	Glume Length	Lemma Length	No. of seeds	No. of Internodes	Seed Length.
103	2.5	8.0	9.5	37	21	5.5
99	2.1	8.0	9.1	31	19	5.6
106	3.2	7.7	9.0	37	21	5.5
110	2.8	8.0	9.4	40	20	5.6
99	3.5	7.4	9.0	35	20	5.1
Average:						
103	2.8	7.8	9.2	36	20.5	5.5

Due to the poor condition of the Marquis heads only five could be used in making an analysis of parent characters. Ten heads of Cornwheat were used but thru an oversight the details for each plant were not preserved and only the average values for the different Cornwheat characters can be given.

DESCRIPTION OF F1 MATERIAL

The heads of Cornwheat X Marquis are slender, somewhat tapering, and from 101 to 132 mm long. They have a large amount of black in the glumes occuring as fine lines and splashes. Many of the glumes are nearly black. A smoky blue over color or bloom is noticeable in all of the heads. It is difficult to tell the source of this color. The very fine short pubescence over the black glumes may partly cause this appearance, but it persists to some extent when the pubescence has been rubbed off.

The glumes are longer than those of the Marquis parent but are not longer than the glumes of some other bread wheats. In shape, they resemble the blumes of Emmer, especially in the sharp keels. They entirely lack the papery appearance of the glumes of Cornsheat and are harder and thicker than the glumes of Marquis.

The exposed parts of the lemma are, as a rule, about the color of the glumes, though some lack the black color. Their beaks are long and sharp, and near the tip of the head, take on the appearance of short awns. Some are of normal straw color and some are black.

The F1 kernels are hard and vitreous and of red, amber color. They are intermediate in length. In shape they resemble Cornwheat more than Marquis.

Table 3.

Detailed Description of F1 Population.

Rachis Length	Awn Length	Glume Length	Lemma Length	No. of seeds	No. of internodes	Seed length
132	3.8	12.3	13.2	11	23	6.6
110	4.0	11.5	12.0	13	22	6.7
131	4.0	12.0	12.4	13	23	6.7
121	3.8	12.0	12.7	18	22	7.2
104	3.5	12.1	11.9	13 ½	20	6.7
125	4.1	13.0	13.6	16	20	7.1
123	4.7	12.6	12.8	20	21	7.1
127	4.1	11.6	12.7	14	22	6.9
132	5.3	12.2	13.0	11	22	7.2
101	4.1	11.0	11.3	11	21	6.1

All measurements are in millimeter.

GENERAL APPEARANCE OF F2 HEADS.

Before a detailed description of the F2 heads was made, they were separated into five groups, according to their general appearance. These groups were further separated into awnless and awned classes. The following table shows these groups and classes after the preliminary separation:

Table 4. F2 Types.

	Polonicum	Intermediate	Vulgare	Durum	Durum Club	Total
Awnless	22	56	15	11	5	111
Awned	6	23	5	4	0	36
Total	28	79	20	15	5	147

Neither true parent type was recovered, although those which are classed as polonicum, as a rule, more nearly resemble the polonicum parent than do those which are classed as vulgare resemble the vulgare parent. All the heads are to a greater or less extent intermediate. All the above classes contained both short and long heads with the exception of the durum and durum club classes. The groups classed as durum and durum club while resembling durum were not distinct durum types but bore a closer resemblance to durum than to either of the parents. The vulgare class contained two heads which very closely resembled Marquis in shape of head and density, but both showed some pubesence. One showed some black in the glumes, though not particularly noticeable. The class as a whole had sharper keeled glumes than true vulgare. All classes, with the exception of the polonicum, contained pubescent heads and heads showing more or less coloring on the glumes, or the awns, or on both. Many of the awned hybrids were much more strongly awned than Cornwheat.

Table 5.

DETAILED DESCRIPTION OF F2 POPULATION

Group	Plant No.	Pub.	Keel Type	Awn length	Glume Color	Awn Color	Glume Length	Seed Length	Seed Color
Int	1	T	S	6.8	B	B	14.1	6.3	R
"	2	G	S	3.6	R	W	15.2	7.3	W
"	3	P	S	11.4	Bl.	B	10.8	6.7	W
"	4	T	S	5.3	R	W	12.5	6.5	R
"	5	G	S	2.8	W	W	12.3	6.1	R
"	6	T	S	12.6	B	W	14.9	6.0	R
"	7	T	S	6.4	Bl	B	14.3	7.0	R
"	8	T	S	4.6	Bl	W	12.5	5.2	R
"	9	P	S	1.0	B	W	14.1	7.0	R
"	10	G	S	-	B	W	13.6	5.8	R
"	11	G	S	1.8	Bl	W	12.4	5.0	-
"	12	G	S	2.6	W	W	14.0	-	-
"	13	T	S	2.6	W	W	16.4	9.0	R
"	14	T	S	3.0	Bl	W	13.2	6.6	W
"	15	P	S	3.0	Br	Br	10.8	6.2	R
"	16	P	S	-	B	B	-	6.4	R
"	17	G	S	1.8	Bl	W	10.2	-	-
"	18	T	S	1.7	W	W	12.7	6.6	R

Group	Plant No.	Pub	Keel Type	Awn Length	Glume Color	Awn Color	Glume Length	Seed Length	Seed Color
Int	19	G	S	-	W	W	15.1	7.6	R
"	20	P	S	2.0	Br	Br	13.1	7.0	R
"	21	G	S	1.3	Br	W	13.9	7.7	R
"	22	T	S	2.6	B	W	13.5	7.8	R
"	23	T	S	4.0	W	W	15.7	6.3	R
"	24	T	S	2.4	B	-	12.9	5.6	R
"	25	G	S	3.0	W	W	14.4	7.3	W
"	26	G	S	6.2	B	W	14.2	-	R
"	27	P	S	1.2	B	B	18.6	-	-
"	28	G	S	5.1	Br	Br	13.2	7.0	R
"	29	T	S	5.3	B	B	15.2	6.9	R
"	30	P	S	5.3	W	W	12.3	6.3	W
"	31	T	S	2.7	Bl	B	12.3	-	-
"	32	G	S	3.2	W	W	17.3	-	-
"	33	G	S	2.4	W	W	16.9	7.7	R
"	34	P	S	3.2	W	W	10.4	7.0	R
"	35	T	S	1.3	B	W	9.6	7.0	R
"	36	G	S	3.8	W	W	13.9	6.8	R
"	37	G	S	5.8	W	W	-	-	R
"	38	G	S	2.5	W	W	12.4	7.2	R
"	39	T	S	3.0	W	W	13.0	-	R
"	40	T	S	-	B	W	11.7	6.6	R
"	41	P	S	-	W	W	-	6.6	R
"	42	P	S	4.7	Bl	W	14.5	7.5	-
"	43	P	S	-	B	W	15.9	7.0	R
"	44	G	S	1.4	W	W	17.6	6.4	-
"	45	G	S	1.0	B	W	17.9	8.0	R

Group	Plant	Pub.	Keel	Awn Leng	Glume Color	Awn Color	Glume Leng.	Seed Leng	Seed Color
Int.	46	P	S	-	B	B	12.4	7.7	R
"	47	G	S	6.4	W	W	15.9	7.3	R
"	48	P	S	0.9	W	B	16.7	7.3	R
"	49	P	S	1.3	W	W	11.8	-	-
"	50	T	S	-	Bl	B	13.3	6.9	-
"	51	P	S	1.3	Br	W	17.4	7.0	W
"	52	T	S	2.6	B	W	16.6	8.1	R
"	53	G	S	5.6	B	B	14.0	7.0	W
"	54	T	S	2.8	W	W	11.2	-	R
"	55	G	S	0.9	W	B	26.0	7.9	R
"	56	G	S	-	W	W	-	-	-
"	57	G	S	78.9	W	B	11.8	6.7	R
"	58	T	S	36.0	W	B	15.1	6.0	R
"	59	G	S	89.5	B	B	15.0	8.0	W
"	60	G	S	34.6	B	B	11.7	6.2	R
"	61	G	S	41.4	W	W	11.5	6.0	R
"	62	G	S	59.6	W	B	14.1	7.0	-
"	63	G	S	66.9	R	W	14.3	7.0	R
"	64	G	S	56.0	W	W	14.5	8.5	R
"	65	P	S	84.6	W	B	10.0	6.5	R
"	66	G	S	49.0	B	B	16.4	5.7	R
"	67	T	S	68.6	R	W	10.0	6.0	R
"	68	G	S	76.9	R	B	13.7	6.8	R
"	69	G	S	57.3	Br	W	11.9	-	R
"	70	G	S	41.3	W	W	12.0	-	-
"	71	T	S	26.3	B	B	14.7	-	R

Group	Plant	Pub.	Keel Type	Awn Length	Glume Color	Awn Color	Glume Leng.	Seed Leng.	Seed Color
Int.	72	G	S	52.6	W	W	14.3	7.1	W
"	73	T	S	-	Br	W	-	-	-
"	74	T	S	46.6	Br	W	9.5	-	-
"	75	G	S	46.5	B	B	20.0	8.6	R
"	76	T	S	50.9	Bl	B	11.3	7.7	R
"	77	G	S	66.2	-	W	14.0	6.2	R
"	78	T	S	71.4	B	B	16.8	6.7	R
"	79	G	S	83.5	-	-	14.8	7.6	R
Pol.	80	G	S	80.8	W	B	17.4	7.7	R
"	81	G	S	49.2	W	W	17.8	7.5	R
"	82	G	S	53.6	W	W	19.5	6.3	R
"	83	G	S	-	B	B	-	6.7	R
"	84	G	S	47.5	W	W	19.2	6.8	R
"	85	G	S	34.3	W	W	15.2	-	-
"	86	G	S	35.5	W	W	17.0	5.0	R
"	87	G	S	-	Bl	W	18.9	8.1	R
"	88	G	S	4.7	W	W	20.9	-	W
"	89	T	S	1.1	Bl	W	22.2	6.0	R
"	90	G	S	1.2	Bl	W	21.6	-	R
"	91	T	S	1.0	Br	Br	16.3	6.6	W
"	92	G	S	-	W	W	22.7	8.3	R
"	93	G	S	1.0	W	W	21.0	8.0	R
"	94	G	S	1.3	Br	W	21.3	7.8	R
"	95	T	S	2.6	Br	Br	16.1	6.4	R
"	96	T	S	1.5	Br	Br	21.1	5.9	R
"	97	T	S	1.4	Bl	W	21.4	-	R

Group	Plant	Pub	Keel Type	Awn Length	Glume Color	Awn Color	Glume Leng.	Seed Leng.	Seed Color
Pol.	98	G	S	-	Br	Br	-	6.6	R
"	99	G	S	3.0	Br	Br	25.3	6.6	R
"	100	G	S	0.7	R	W	18.9	7.0	R
"	101	G	S	5.0	W	W	21.4	6.9	R
"	102	G	S	3.1	W	W	17.8	6.1	R
"	103	G	S	2.5	Br	W	19.6	6.7	R
"	104	G	S	1.3	W	W	17.4	7.6	W
"	105	G	S	2.3	W	W	27.3	6.1	R
"	106	G	S	1.9	Br	Br	22.6	7.6	R
"	107	G	S	1.0	W	W	15.8	-	-
Vul.	108	G	S	4.1	Br	Br	9.8	6.4	R
"	109	G	S	1.3	Br	Br	9.8	6.1	R
"	110	G	S	2.7	R	W	11.3	7.0	R
"	111	P	D	2.4	Br	Br	10.1	6.5	R
"	112	G	S	0.8	W	W	10.7	6.5	R
"	113	P	S	1.8	Br	Br	9.9	6.1	R
"	114	G	S	2.7	-	-	10.7	6.9	R
"	115	P	S	7.3	Br	Br	10.3	7.3	R
"	116	G	S	5.4	W	W	10.0	7.1	R
"	117	P	S	2.0	R	R	12.0	6.7	R
"	118	G	D	7.0	W	W	10.5	6.2	R
"	119	P	S	0.2	W	W	8.9	-	-
"	120	G	S	1.4	R	R	9.1	7.1	-
"	121	G	S	0.9	W	W	10.2	-	-
"	122	G	S	11.2	-	-	8.9	6.0	R

Group	Plant	Pub	Keel	Awn Length	Glume Color	Awn Color	Glume Leng.	Seed Leng	Seed Color
Pol.	123	G	S	1.3	W	W	10.8	-	-
"	124	G	S	0.8	-	-	7.7	-	-
"	125	P	S	3.9	R	W	9.7	5.3	-
"	126	P	S	69.2	B	B	9.3	6.1	R
"	127	P	S	62.6	Br	Br	11.4	6.5	R
Durüm	128	G	S	1.5	W	W	9.5	6.1	-
"	129	P	S	3.4	R	W	10.6	7.0	R
"	130	T	S	1.6	Bl	W	12.8	6.0	R
"	131	P	S	1.3	R	W	11.2	-	-
"	132	P	S	5.6	Br	Br	9.3	6.7	R
"	133	P	S	1.3	B	B	11.5	5.8	R
"	134	T	S	4.0	W	W	11.9	6.3	R
"	135	T	S	2.7	-	W	9.1	5.7	R
"	136	P	D	71.3	W	B	10.3	6.4	W
"	137	P	D	2.5	W	B	9.3	-	R
"	138	P	S	2.6	R	B	9.4	4.8	R
"	139	G	S	2.4	R	W	13.9	7.0	R
"	140	G	S	79.4	R	B	9.9	5.8	W
"	141	G	S	78.2	-	-	8.8	5.0	W
"	142	G	S	70.7	R	B	8.5	5.8	R
Clubs	143	G	S	5.4	Br	W	9.7	6.6	R
"	144	P	S	1.2	R	W	8.5	-	-
"	145	P	S	2.7	B	B	9.3	6.5	R
"	146	P	S	1.2	B	B	8.5	5.3	W
"	147	P	D	1.6	Br	Br	8.3	-	-

Legend------

P-	Indicates	pubescent
G-	"	glabrous
T-	"	trace of pubescences
S-	"	sharp keel
D-	"	dull or vulgare type keel
B-	"	black color
Bl-	"	blue-black
Br-	"	brown
R-	"	red
W-	"	white

Plate 1

Parent and Hybrid Types

DESCRIPTION OF F3 POPULATION.

The F3 population resembled the F2 excepting that no club type heads appeared. In the two head rows grown from clubbed heads, only long heads were produced. Some of the heads resembling durum were more or less intermediate in appearance between true durum and spelt, and durum and emmer types. This was more noticeable in the F3 than in the F2 generation. Plate 1 illustrates characteristic types of F3 segregations. In the top row is shown heads of the two parents, Marquis on the left and Cornwheat on the right, with an F1 head between. The middle row is of durum segregates and intermediate types between durum and emmer, and between durm and spelt. It will be noticed that the head on the extreme right resembles emmer somewhat, while the third head from the right has the long internodes of the rachis characteristic of spelt. On the left of the bottom row are two heads of vulgare type, the two on the right closely resemble polonicum, while the middle two are intermediate to the two parent types. Only a few polonicum type plants have glumes as long as true polonicum. The papery condition of the glumes of true polonicum seems to be entirely recovered in a small number of F3 heads. The F3 population as a whole is characterised by a great multiplicity of forms which range from those closely resembling polonicum thru every gradation of intermediate to heads which to all appearances are true vulgare. Although a comparatively few heads closely approach the true polonicum type a very great proportion distincly show polonicum characters. A comparatively small number of heads are distinctly vulgare. The durum segregates make up a fairly large group.

CHARACTERS STUDIED.

Detailed data for the following seven head characters were taken from the parent and F1 material: Rachis length, awn length, glume length, lemma length, number of seeds, number of internodes, and seed length. Detailed data were taken from the F2 and F3 generations for the following twelve characters: pubescence, keel type, rachis length, awn length, glume color, awn color, glume length, lemma length, number of seeds, number of internodes, seed length, and seed color.

The study of the inheritance of eight of these characters is presented in this thesis. They are pubescence, keel type, awns, glume color, awn color, glume length, seed length, and seed color.

Detailed data covering the above eight characters are included under "Description of Material". On account of its bulk, the corresponding data for the F3 generation has been omitted. However, liberal use of the F3 data has been made in the preparation of tables and in making interpretations. These data may be found in the files of the Farm Crops Department, State College of Washington.

HOW THE DATA WERE TAKEN.

All measurements appearing in the data connected with this study are given in milli-meters. In determining awn length and glume length, five measurements were taken ranging from the base to the tip of the head. The length for glumes and awn as appearing in the data is the average of these five measurements. In the case of seed length all seeds in the head were measured if the number was less than ten, otherwise ten representative seeds were measured and the average determined. Heads with badly shriveled seeds were not used in determining seed length.

In determining pubescence all plants with glumes appearing velvety to the naked eye were classed as pubescent. All others were examined with a hand lens. Those showing pubescence in this way were classed as having a trace of pubescence, and those remaining, as glabrous.

REVIEW OF LITERATURE.

From published accounts, it is evident that Triticum polonicum seldom has been used to cross with other wheats. This is not surprising considering its slight economic importance. There is no record, to my knowledge, of any crosses between varieties of T. polonicum.

Percival (16) , in his monograph on the Wheat Plant, gives a classification of T. polonicum containing twenty-three varieties. These varieties differ considerably in a number of characters. Five glume colors occur; white, pale red, black, pale violet, and blue-black. Both glabrous and pubescent forms exist in both white and colored glumed varieties. The varieties also differ in length of awns and color of awns. The awn colors listed are White, black and pale red. Other differing characters are head length, shape of head, compactness and seed color. In further discussing polonicum characters, Percival says: "Branching of the ear is uncommon in T. polonicum, but occurs occasionally." He then sights the variety "deformatum" described in Seringe as one showing this character.

Investigators generally have attributed the inheritance of pubescence on the glume to a single factor. Biffen (2) found that pubescence is inherited as a dominant character in T. vulgare and that it segregates in a 3:1 ratio in the F2 generation. In crosses between T.turgidum and T. vulgare, he found that the dominance is irregular. None of the F1 plants were as pubescent as the turgidum parent, while many appeared glabrous to the naked eye, and showed pubescence only when a lens was used. None were perfectly glabrous, however. In the F2 generation the plants segregated for approximately 3 pubescent to 1 glabrous. The Howards (11) have reported that there are two independently inherited factors for pubescence in Indian wheats. One causes a long pubescence, the other a short pubescence. When both factors are present a densely pubescent plant results.

The glumes of vulgare varieties of wheat are characterized by a dull keel which often fails to extend entirely to their base. The glumes of other cultivated wheats have sharp keels extending along the entire length of the glume. In a cross sighted by Biffen (2) the sharp keeled condition is dominant over that of the vulgare type andthe F2 segregates in a 3:1 ratio. Sax and Gaines (18) report a cross in which the vulgare type keel is dominant over sharp keel

Some confusion has been casued by literature on the inheritance of awns owing to what might be termed tip-awned plants, generally being referred to as awnless. The majority of our so called awnless wheats are of this class. Wheats occur which are completely awnless.

In the Washington bulletin on "Inheritance in Wheat, Barley and Oat Hybrids", Gaines (8) makes the following distinction between "bearded" and "beardless" wheats: "In some wheats the upper end of the floral glume terminates in a needle-like awn which varies in length from one to four inches. In other wheats known as beardless, the floral glume ends in a curved beak less than half an inch in length. In some beardless varieties, the beaks may assume awn-like appearances on the floral glumes near the apex of the spike and may reach a length of an inch or more." There is a marked difference between truly awnless wheats and the "beardless" wheats described above.

In wheat crosses made by Biffen (2), he obtained three awnless to one awned plant in the F2 generation. In reciprocal crosses between a bearded vulgare and a beardless club Gaines (8) obtained F1 generations that had short awns and F2 generations segregating for awns to a 1:2:1 ration.

The Howards, working with Indian wheats, were the first investigators to publish a complete explanation of the inheritance of awns in wheat. This is set forth in two articles (11) and (12) "On the Inheritance of Some Characters in Wheat." These were published in 1912 and in 1915 respectively. The first reported that the existance of two factors for bearding had been observed. In crosses between fully awned and tip-awned varieties, the F1 was intermediate, having short awns. The F2 generation produced fully awned, intermediate, and tip-awned in a 1:2:1 ratio. Fully awned crossed with awnless (without tip awns or beaks) gave an F1 generation with tip awns and an F2 consisting of awnless, short tipped, long tipped, half awned, nearly full awned and fully awned. Considering the tipped plants as awned, the ration was 15:1.

In their second paper the Howards go into considerable detail on the inheritance of awns. In effect, their explanation is that there are two independently inherited factors either of which may cause tip awns. One causes long tips, the other short tips. When these factors occur together, they produce the fully awned condition. "In the long tip plant the beards are only found near the tip of the ear, where one is often much longer than the rest. In the short tip plants, the beards are more or less the same length and are generally uniformly distributed over the upper two-thirds of the ear.". The short factor serves to distribute foundations of bearding over the whole head and the long factor serves as an intensifier. These investigations were carefully worked out in detail and were carried thru the F4 generation.

Harrington (9) has reported work on the inheritance of awns in two wheat crosses that confirms the work of the Howards.

The inheritance of glume color has been reported on by several workers. Biffen (2) found that in crosses between red chaff and white chaff vulgare wheats, that red was inherited as a simple dominant, there being 3 red to 1 white in the F2 generation. In crosses between grey chaffed turgidum wheats and white chaffed vulgare varieties, grey was dominant, but the amount of grey in the F1 varied with the cross. In crosses between T. polonicum and red chaffed wheats reported in a later paper (3) the F1 plants had red glumes and the F2 produced red and white glumed plants in the ratio of 3:1.

In all crosses of red X white glumed wheats observed by the Howards (11) the inheritance of glume color was due to a single factor. In the case of awn color, they report ratios approaching three black to one white. The development of awn color is probably affected by environment more than that of glume color. "In many Indian wheats if premature ripening takes place awn color is not developed".

The inheritance of glume length has very naturally attracted the attention of all those who have worked with crosses involving Titicum polonicum. As yet no entirely satisfactory explanation of its mode of inheritance has been given. In a cross of Polish X Rivet (turgidum) made by Biffen (2) the F1 was intermediate for glume length and the F2 ranged from short to long in such a manner that they were difficult to classify off hand. Arranged in a curve, a 1:2:1 ratio was apparent. Caporn (4) has reported work on a cross of T. polonicum X T. eloboni in which the F1 glume length, while intermediate, ranged from glumes slightly longer than eloboni to others a little shorter than the minimum polonicum glume". In the F2 generation, while certain heads were clearly long or short glumed, there was a very large proportion which verged on these extremes, as well as those which were obviously intermediate. When plotted the glume lengths produced a three peak curve indicating homozygous shorts, homozygous longs and heterozygous short-longs. There were 170 F3 rows with a sufficient number of plants per row to permit accurate classification. These segregated to a 1:2:1 ratio.

In crosses of T. polonicum X T. durum and turgidum, Bakchouse (1) reports results for the inheritance of glume length that closely agree with those obtained by Biffen in his crosses of Polish X. Rivet.

Engledow (7) obtained similar results in the cross Polish X Kubanka (durum). The F2 generation segregated for long, intermediate, and short in the ratio of 1:2:1. The "longs" and "shorts" of the F2 altho recognizably of the same form as the parents, different from them in mean glume-length. The average of the longs was reduced by 24.8 percent of the F0 value. In the case of the F2 shorts there was an increase over the parent shorts but it was smaller. This change or "shift" in the longs was quite definite and cannot be explained by errors of sampling, seasonal variation or any such cause. The "shifted" form of the longs bred true in the F3 generation. F3 segregates of parental type grown from the seed of F2 heterozygotes showed no evidence of any added "shift". Likewise, there was no tendency toward the restoration of the F0 values of mean glume length.

Percival (16) states that in a natural cross, between T. polonicum and T. dicoccum he observed that the long and short glumed homozygotes were readily distinguishable from the intermediate heterozygotes, and in commenting further, says, "but where the second parent is a durum or turgidum it is practically impossible to classify the F2 generation into three groups by eye inspection alone, since the ears obviously short-glumed and long-glumed are always connected by a closely graduated series of intermediates."

A cross of T. polonicum X T. vulgare was obtained by Tschermak (20) in which the F1 plants had intermediate glume length. In the F2 generation polonicum, intermediate and vulgare forms were obtained. The vulgare form had glumes somewhat longer than those of the vulgare parent. In addition to the above forms, a small number of new durum forms appeared. Neither of the polonicum nor the vulgare forms in this or subsequent generations were exactly like the parents of the cross. From results obtained Tschermak explained the inheritance of long glumes in this cross on a basis of two main factors. His explanation was that polonicum has two dominant factors for long glume and that durum carries a single one of these factors, while the recessive allelomorphs of both these factors are carried by vulgare. This hypothesis, to my knowledge, has not been proved or disproved.

Percival (16) is of the opinion that Triticum polonicum represents a mutation of T. durum. He sights many similarities between these species supporting his conclusion, and further says "I have seen occasional specimens of Indian durums with elongated glumes suggestive of incipient polonicum, and Kornicke states that Schweinfurth sent him from Upper Egypt a transition form between durum and polonicum". He somewhat modifies the above conclusion by observing that, "the lax ear, long spikelet, glumes and grain of Krorasan wheat suggest a variation towards the production of a polonicum from the pubescent-leaved dicoccoides or Indo-Abyssinian dicoccum."

In grain length, (Biffen (2) found no indication of the dominance of either the short or the long grain character in repiprocal crosses of Polish and Rivet wheats. The F1 grains corresponded in shape and color to those of the female parent. The F2 grain (F1 plants) produced by the reciprocal crosses were identical. They were intermediate between those of the parents. The F3 grains (F2 plants) segregated into short, intermediate, and long in the ratio 1:2:1.

Engledow (7) has found that the inheritance of seed length in his Polish X Kubanka cross, to which reference has already been made, closely parallels that of glume length. In the F2 plants there was segregation of seed length for short, intermediate, and long in the ratio of 1:2:1. The shorts and the longs showed a "shift" similar to that described for glume length. That is, seed of the short seeded segregates were longer than those of vulgare, while those segregating for long seed had shorter seed than polonicum.

The study of the inheritance of red color in the seeds of wheat has presented comparatively few difficulties. Biffen (2) in 1905 found that in vulgare crosses with which he was working that red seed color was due to a single dominant factor. In studies made by Harrington (9) he found that "the ratio of red-seeded to white-seeded plants in the F2 approached 3:1 in some cases and 15:1 in others." Hayes and Robertson (10) found two factors for red seed color in Marquis and three factors in some other varieties. The Howards, (11) found that red color of grain in Indian wheats is due to one, two or three independent factors. Each produces red coloration but the shade varies. The effect of these factors is cumulative. Gaines (8) has obtained similar results in crosses of American varieties.

The existance of factors which may modify, or in some instances entirely inhibit the expression of certain characters has been demonstrated in a considerable number of cases. On the whole they form a group of which little is known. Gaines (8) describes a partial suppression of awning in a cross between a bearded vulgare wheat and a beardless club. In the bearded club segregates, the awns were about half as long as in the bearded vulgare segregates. The classification of American wheat varieties issued by the United States Department of Agriculture (5) lists but one fully bearded club wheat. In this variety Mayview club, the awns are short like those in the bearded club segregates, described by Gaines.

In reciprocal crosses of T. polonicum and T. turgidum, Biffen (3) found pubescent chaff only among the segregates having short or intermediate glumes. The long glumed segregates were practically glabrous. In these crosses all plants in the F2 and later generations had glumes of a color indentical with that of the Polish parent. There was no segregation for the grey color of the turgidum parent. Other colored wheats crossed with T. polonicum gave different results. In these, segregation for color occured in the F2 generation, but color was confined to plants with short or intermediate glumes. Biffen sights as other examples of the suppression of characters an instance where two beardless wheats were crossed and produced in the F2, one bearded to three beardless plants, and another instance in which white seed appeared in the F2 of a cross of two red seeded wheats..

In crosses of T. polonicum with T. durum and turgidum, Backhouse (1) found that among the short glumed segregates the ratio of pubescent plants to glabrous was 3:1. In the plants with intermediate glume-length he obtained 85 felted to 31 smooth. Among 56 long-glumed plants, the theoretical expectation of homozygous longs, and beginning at the extreme long end of the curve, no "felted" glumes were found, tho with a lens a short velvety pubescence could be seen on most. Selections of long-glumed segregates as glabrous as Kubanka were made by the use of a hand lens and grown in the F3 to determine the pure longs. The latter were crossed with Kubanka and other durums to see if pubescence was in any way effected by the segregation of glume length. In the F2 generation some were all smooth while others gave 3 pubescent to 1 smooth among the short glumed segregates, proving to the satisfaction of Backhouse that the long glume of polonicum inhibits pubescence.

Engledow (7) reports observing that in a cross of Polish X Kubanka a development of hairs far more marked than that exhibited by either parent variety was found in certain of the F2 plants. These plants were all of short glume type. Length of glume appears in some manner to inhibit the full development of hairs.

Pubescent segregates have occured in the progeny of crosses of Kubanka X. Bluestem (vulgare) obtained at the Washington Experiment Station (21)

The occurence of abnormalities in the progeny of species crosses of wheat has been reported from time to time by various workers. Biffen (3) has reported that the F2 generation of crosses of Polish and Rivet wheat is "characterised by the occurence of a bewildering, tho evidently definite, series of unexpected forms such for instance as plants with bright grass green instead of glaccous foliage, with ears of the spelta type, with branching ears, dwarfs, etc."

Percival dexcribes the occurence of two spikelets to a single joint in the rachis. He mentions two ways in which they occur; first, the adventitious spikelet; beside and at right angles to the normal spikelet; and second, protruding from the same joint of the rachis just beneath the normal spikelet. Coffman (6) mentions a like condition in what he terms "supernumerary spikelets in Mindum wheat".Kajanus (13) describes the second type of extra spikelet mentioned by Parcival as occuring in a cross of T. vulgare X T spelta. He reports it as behaving as a recessive. Nilsson-Leissner (15) has found both types of additional spikelets in the progeny of two crosses of T. Spelta and T. vulgare. The occurence of the additional spikelet at the side of the normal spikelet was rare; while the other type, in which the additional spikelet protrudes from the rachis beneath the normal spikelet, was found often in the two crosses.

He says "Increase of ear density and improvement of nutrition conditions result in an increasing percentage of plants with additional spikelets as well as an increasing number of these anomalies per ear. The character is recessive and probably due to several genes."

Nilsson-Leissner in the paper just referred to, describes three other abnormalities occuring in his crosses. Instances occur where one or two flowers in one or several spikelets are replaced by whole spikelets. Another type of abnormality is the "bifurcated rachis". In a third type, some of the spikelets are replaced by whole branches having up to seven spikelets. He finds that the appearance of this type is to a great extent due to the modifying influence of environment. He concludes that it is probably recessive and dependent on several multiple factors.

THE INHERITANCE OF PUBESCENCE ON GLUMES.

Both cornwheat and Marquis have smooth chaff. From this we might reasonably expect the offspring of a cross between them to breed true for this character. However, plants of the F1 generation bear heads having a very short fine pubescence and the F2 segregate for pubescent and glabrous glumes.

Backhouse (1) and Biffen (3) each report crosses between Triticum polonicum and T. turgidum in which this phenomenon occurs and where segregation for pubescent and glabrous chaff takes place in the F2 generation. Their explanation is that T. polonicum carries a factor for pubescence, the expression of which is inhibited by the factor for long glumes as only short glumed segregates were distinctly pubescent. Polonicum likewise carries a factor for glume color which is similarly inhibited.

In the Cornwheat X Marquis cross, the F2 generation segregated for pubescent, glabrous, and an intermediate type similar to the F1. All apparently glabrous heads were examined with a hand lens. Only those which retained their glabrous appearance under the glass were classed as glabrous. Those heads which were plainly pubescent to the naked eye were recorded as pubescent, while those in which the pubescence was determined by the aid of a lens were recorded as having a trace of pubescence. All the latter would normally be classed as glabrous in the usual manner of making separations. According to the above separations, there were 78 glabrous heads, 35 pubescent heads, and 34 heads showing a trace of pubescence. If both the pubescent heads and those showing a trace of pubescence are classed as pubescent, we have 78 glabrous to 69 pubescent, or reduced to its lowest terms, the ratio of 1.13:1.

The following table shows the occurence of pubescence in the different groups segregating in the F2 generation:

Table 6.

Group	Pubescent	Trace	Glabrous	No. of plants.
Polonicum	0	5	23	28
Intermediate	16	26	37	79
Vulgare	8	0	12	20
Durum	7	3	5	15
D. Club	4	0	1	5
Total	35	34	78	147

This table illustrates the action of the inhibitor referred to above. Only five of the 28 polonicum segregates showed any trace of pubescence. At a casual glance these five heads all appeared to be glabrous but an examination with a lens showed them to have a trace of pubescence. In none was the pubescence as noticeable as it was in the F1.

The vulgare and club segregates, from all appearances, were either distinctly pubescent or perfectly smooth. The durum and intermediate groups segregated for all three classes, having heads that were distinctly pubescent, other with only a trace of pubescence, and still others that were completely glabrous. The proportion in which these segregations occured was distinctly different in the two groups showing a decidedly greater tendency toward suppression of pubescence in the intermediate group than in the durum group.

The F3 plants were examined for pubescence in the same manner in which the F2 data for this character were taken. Of 623 plants of the F3 generation, having pubescent glumes, 397 were distinctly pubescent while 226 showed only a trace of pubescence, while 428 were glabrous. Grouping the two types of pubescence, together gives 623 plants with pubescent glumes to 428 with glabrous glumes, or reduced to its lowest terms, the ratio becomes 1.45 pubescent to 1 glabrous. The F3 plants were grown in head rows, each row being the progeny of one head from an F2 plant. The heads for planting were selected entirely on the basis of fertility as indicated by the number of grains they contained, With one or two exceptions, only seed from heads having ten or more grains were planted. Beyond this there was no selection, except for the inclusion of one or two highly sterile heads selected for a special purpose.

The following table shows the distribution of the head rows in relation to the group segregations in the F2 generations:

Table 7.

F2 Plants					F3 Head Rows.			
Group	Pub.	Trace	Glab.	Total	No. Breed true Pub.	Trace.	Glab	Break up.
Polonicum	0	3	11	14	0	0	1	13
Intermediate,	8	15	10	33	#2	0	5	26
Vulgare	5	0	5	10	0	0	3	7
Durum	2	0	2	4	1	0	0	3
Durum Club	2	0	0	2	1	0	0	1

One row grown from a pubescent F2, matured but a single pubescent plant.

All F3 rows producing more than a single plant and descending from F2 plants showing but a trace of pubescence, with a single exception, produced both pubescent and glabroud plants. One row, (No. 1744) produced fifteen plants, eight being distinctly pubescent and seven showing but a trace of pubescence. Not a single F2 plant showing but a trace of pubescence bred true to this character in the F3 generation.

At the time I was working on the F2 data, it was suggested that I was probably dealing with two genetically distinct types of pubescence, such as have been peported by the Howards (11). The F3 data proves that in the Cornwheat X Marquis, cross both kinds of pubescence found are due to an identical factor or factors, and that their difference is the result of the action of an inhibitor or inhibitors carried by polonicum.

Laying aside the possibility that the heterozygous glabrous plants in the vulgare and durum groups were wrongly described when the F2 data were taken, it seems likely that their appearance was due to an inhibitor inherited from polonicum. As none of these heads had long glumes, nor produced long glumed progeny, it seems reasonable to conclude that the inhibitor for pubescence is not the same as the factor for long glumes, although closely linked.

INHERITANCE OF KEEL TYPE

Cornwheat has narrow glumes with sharp keels reaching to the base of the glumes. Marquis has broader glumes and dull keels. These often terminate above the base of the glume. In the F1 generation all plants had narrow glumes with sharp keels reaching to the base of the glume. In the F2 generation there were 142 plants having sharp keels and 5 with vulgare type keels, a ratio of 28.4 : 1. F3 head rows were planted from three of these five plants with vulgare-like keels. In examining the F3 material, it was noticed that the majority had sharp keels reaching to the base of the glumes like those of Cornwheat. In some plants the upper part of the glume was narrow and sharp keeled but the lower part of the glume was rounded like that of vulgare. These were designated as intermediate when the F3 data were taken. In addition to the above classes a considerable number of F3 plants had distinctly vulgare-like keels. The number of plants segregating according to the above classes was 917 sharp, 67 intermediate, and 65 vulgare-like. Of the 63 rows of F3 plants, 60 were grown from F2 plants with sharp keels. Of these, 34 produced only sharp-keeled plants, while the others broke up in varying proportions as shown in Table 8. Of the three rows grown from plants with dull keels, one bred true and two broke up.

In the following table "S" indicates sharp keels and "D" dull keels.

Table 8.

Row No.	F2 Keel Type	F3 Plants S	I	D
1705	S	8	0	0
1706	S	13	1	0
1707	S	5	3	1
1708	S	26	0	1
1709	S	19	1	1
1710	S	7	2	0
1711	S	10	0	0
1712	S	7	1	1
1713	S	16	1	2
1714	S	2	4	7
1715	S	20	3	2
1716	S	31	0	0
1717	S	11	0	0
1718	S	26	2	1
1719	S	25	0	0
1720	S	38	0	0
1721	S	1	0	0
1722	S	16	0	0
1723	S	22	0	0
1724	S	1	4	2
1725	S	18	0	0
1726	S	20	1	2
1727	S	12	0	0
1728	S	17	0	0
1729	S	35	0	0
1730	S	11	1	0
1731	S	1	0	0
1732	S	9	0	0
1741	S	13	0	0
1742	S	18	0	0
1743	S	17	0	0
1744	S	15	0	0
1745	S	26	0	0
1746	S	20	0	0
1747	S	13	0	0
1748	S	28	0	0
1749	S	10	0	0
1750	S	31	1	0
1751	S	31	0	0
1752	S	20	0	0
1753	S	7	0	0
1754	S	22	0	0
1755	S	19	0	0
1756	S	14	0	0
1757	S	5	0	0

Table 8 cont'd

Row No.	F2 Keel Type	F3 Plants S	I	D
1758	S	3	3	0
1759	S	3	1	0
1760	S	4	5	6
1761	S	0	4	12
1762	D	17	1	2
1763	S	15	2	1
1765	S	12	1	0
1766	S	3	1	1
1767	D	0	0	17
1768	S	13	2	0
1769	S	5	7	5
1770	S	7	0	0
1771	S	17	1	0
1766	D	26	6	0
1777	S	22	9	1
1779	S	16	0	0
1780	S	8	0	0
1781	S	12	1	0

INHERITANCE OF AWNS.

The average length of awns in the Cornwheat parent in this cross was 105 mm. The heads were fully awned from base to tip of head. While Marquis is commonly classed as an awnless wheat it has short apical awns and sharp beaks on the sides of the head. Apcial awns 10 mm. in length are not uncommon. The average length of all beaks and apical awns in the Marquis parent was 2.8 mm. The F1 plants had noticably longer apical awns and beaks than the Marquis parent but exhibited a strong dominance of the awnless character. The extremes in average awn length among the different F1 heads were 3.5 and 5.3 mm. The average for the whole F1 population was 4.1 mm.

Table 3 shows the entire range of awn length for the F1 generation.

The F2 generation (table 5) produced 109 plants with heads having short beaks and short apical awns similar to those of Marquis, while three plants were somewhat intermediate with average awn lengths of 11.2, 11.4, and 12.6 respectively. The ratio is as nearly 3 awnless to 1 awned as could be expected in a population of 147 plants. However, many of the awned F2 plants had awns decidedly shorter, thicker and stiffer than the awns of the Cornwheat parent. The extreme awn length in the F2 generation was 89.5mm as against an average of 105 in the Cornwheat parent.

In the F3 generation all head rows grown from the fully awned plants bred true for this character.

THE INHERITANCE OF GLUME COLOR.

Cornwheat has very light straw colored glumes which are usually referred to as white. When crossed with white glumed vulgare wheats, the F1 have colored glumes and the F2 segregate for colored (usually black) and white glumes, (19). This indicates that the factor inhibiting pubescence or a similar factor, also inhibits the expression of glume color. However, it is not as potent in its effect on the suppression of color as on the suppression of pubescence, for while the F1 of crosses between polonimum and other glabrous wheats is only faintly pubescent, the F1 of other crosses between polonicum and other white glumed wheats may be nearly black in color. It is evident then that the inhibitor of glume color is effective only when in the homozygous condition, while the inhibitor of pubescence has a very pronounced effect when in the heterozygous condition.

While Marquis has glumes only slightly darker than those of Cornwheat, the F1 plants have nearly black glumes with a peculair smoky-blue cast. This bluish color has not been mentioned by other investigators as occuring in polonicum crosses. Percival (16) lists a single polonicum variety of this color. The cause of this bluish color is very puzzling. As suggested earlier, it possibly is due to a very fine pubescence over a black glume, but this seems unlikely. This strange color persists to the third generation.

In the F2 generation five different colors for glumes occur: black, brown, red, white and the above mentioned color. The following table shows the number of plants of each occuring in the different groups of segregates:

Table 9.

Group	Bl.	Bluish	Br.	Red	White	Not Class'f'd	Total
Polonicum	1	4	8	1	14	0	28
Intermed.	22	11	8	5	31	2	79
Vulgare	1	0	6	4	6	3	20
Durum	1	1	1	6	4	2	15
Dur. Club	2	0	2	1	0	0	5
	27	16	25	17	55	7	147

Number colored - 80
Number White - 55

Many heads were extremely difficult to classify for color. For instance, some glumes had a body color of brown or red with distinct black stripes or splashed thru it. All heads with such glumes classed as black. Then too, there were all gradations of the bluish color from heads where the color was unmistakable to others where there was only a suggestion of color. This fact should be kept in mind when examining the F3 data.

In the F2 generation, the occurance of plants with bluish glumes is, with one exception, confined to the intermediate and polonicum groups. As these groupings were made only on general appearances, and as all plants of the F2 generation were to a greater or less extent intermediates when compared with the parents, it seems probable that these bluish plants are genetically black. They might be either heterozygotes for the black color factor, or heterozygotes in reference to the inhibitor for color, or may contain a single dose of each factor. The fact that all F1 plants show this bluish color would indicate that the last is probably the true explanation. This theory is supported by an examination of the F3 data. While there was a faint hint of this bluish color in a number of plants scattered thru the F3 population, in only one row did definitely bluish heads occur. This row produced twenty-two plants, four of which had heads of a bluish color which closely resembled F1 heads excepting that one had distinctly longer glumes than were found in heads of F1 plants. The plant from which this row was grown was from the intermediate group and had black glumes. None of the bluish glumed F2 plants produced F3 plants with bluish glumes, the F3 progeny being identical with that of black glumed plants.

The data show clealy the correlation between the inhibitor of color and the factor for long glumes in the preponderance of white glumed plants in rows grown from the F2 plants of the intermediate and polonicum groups as compared with rows grown from plants of other groups. Of a total of 775 plants descended from the intermediate and polonicum groups of the F2 generation, 535 have white glumes and only 240 have colored glumes. Reduced to its lowest terms, the ratio for the offspring of the long-glumed F2 is 2.23 with white glumes to 1 with colored glumes. Among the plants descended from groups distinguished by short glumes, there are 121 plants with white glumes to 130 with colored glumes, a ratio of 1 : 1.07. There probably is linkage between the determiner for long glumes and the inhibitor of glume color but considerable crossing-over takes place.

None of the F2 plants with colored glumes bred true for glume color in the F3 generation. From the way the date for the F2 generation were taken, we could reasonably expect a considerable number of plants classed as black glumed to throw plants with brown or red glumes. This actually happened.

The manner of the classification of the F2 for glume color fails to explain why plants with brown or red glumes should produce offspring with black glumes. This also occured. If the brown and red colors found are due to separate color factors, they are centainly recessive to black as there was nothing to indicate the presence of either of these colors in the F1 population. On the supposition that they are due to separate color factors, we could expect these colors to segregate for white but not for black. When we consider this irregular behavior of the glume colors in the generation, it seems likely that all glume color in this cross is due to a single color factor and that the browns and reds appearing are due either to environmental conditions or other modifying factors.

INHERITANCE OF AWN COLOR.

In cornwheat, both black and white awns occur. The apical awns of Marquis are about the color of the glumes.

The F1 heads have short awns near the tips somewhat longer than the apical awns of Marquis. About the same irregularity in color is found in them as occurs in the awns of cornwheat. The F2 generation shows a segregation for awn color in the proportion of 1.25 colored to 1 white in plants with awns more than 10 mm. long. The colors black, brown, red and white, occur. The range of color is the same as that in the glumes excepting that there is no hint of the bluish color that is so noticeable on the glumes.

Awn color behaves in the F3 generation very similarly to glume color except that there is a larger proportion of the whites that breed true.

THE INHERITANCE OF GLUME LENGTH.

The average glume length of the Cornwheat parent was 27 mm. and of the Marquis parent 7.8 mm. The glume length of the F1 plants ranged from 11 to 13 mm., the average being 12.03 mm. This is 5.37 mm. less than a true intermediate and 4.23 mm. greater than the mean of the short parent.

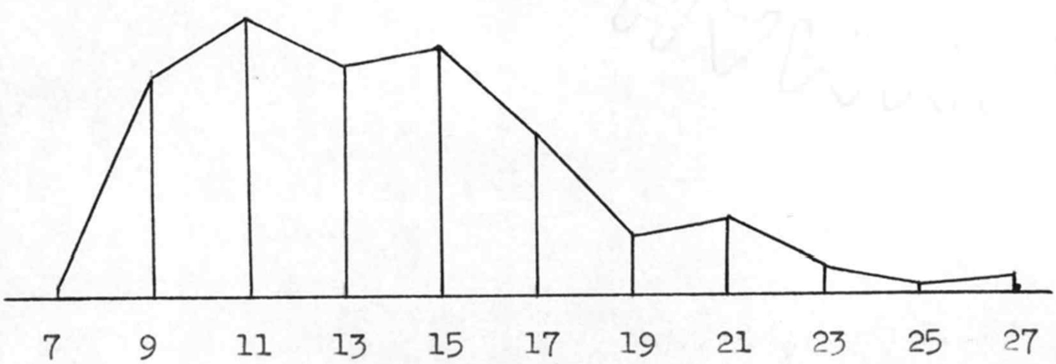
In crosses of Triticum polonicum X T. durum and turgidum, Backhouse (1) obtained F1 generations with a glume every closely approaching a true intermediate. The F1 data in the Cornwheat X Marquis cross indicates that the factors controlling glume length in vulgare behave differently from those controlling glume length in durum and turgidum.

Glume length in the F2 generation ranged from an average of 7.7.mm. for the head having the shortest glumes to an average of 27.3 mm. for the longest glumed head. The plant with a glume length of 7.7. mm. was the only plant having glumes as short as the average glume length of the Marquis parent. Similarly, only one plant had glumes averaging as long as the average of the Cornwheat parent.

While there was F2 segregation for short, intermediate, and long glumes, the heads from their appearance could not be arranged into these three classes due to a large number of intermediates bordering on the short or the long.

Figure 1

F2 Glume Length



The curve shown in Figure (1) represents the segregation of glume length in the F2 population. It suggests a short, an intermediate, and a long class. However, the short and the long classes do not coincide with the glume length of the Marquis and Cornwheat parents. Each class shows a shift toward the intermediate.

This curve is interesting when compared with the F1 glume length of 12 mm. It will be noticed that the highest peak in the curve does not occur as might be expected at the class corresponding to the average F1 glume length but at the next lower class. This is probably due to an overlapping of classes which causes a piling up effect at this part of the curve. The curve also suggests a partial dominance of the short glume factor or factors. However, in considering dominance as indicated in this figure, or in considering any other data pertaining to this cross, due allowance must be made for the difference in fertility between the parents, and the high degree of sterility in intermediate hybrids, The calculated fertility of Cornwheat was only 46.6 per cent while that of Marquis was 87.8 per cent.

The range of glume length in the F3 generation was even greater than that occuring in the F2. The extremes in the average glume length per head were 6.6 and 33.4 mm. Arranged in classes according to the parent group in the F2, the F3 generation shows the following variations:

Table 10.

F2 group	No. of rows	F3 Extremes mm.	Variation mm.
Intermediate	33	7.0 to 28.8	21.8
Polonicum	14	8.6 to 33.4	24.8
Vulgare	10	6.6 to 14.2	7.6
Durum	4	7.8 to 11.8	4.0
Durum Club	2	8.2 to 11.2	3.0

It will be noted that the extremes of the plants in rows descended from the polonicum segregates are more widely separated than those descended from any other group. However, an examination of the F3 data shows that on the whole, these rows are far more regular for glume length than those descended from intermediate plants. While the intermediate group is the most variable, all groups show a decided tendency to break up for glume length.

Table 11 is made up from selected groups of F3 head rows arranged for studying the inheritance of glume length in respect to that of the F2 parent. The first group is composed of rows descended from short glumed F2 plants. The next group is descended from plants having an intermediate glume length. The last group is composed of the offspring of long glumed F2 plants. In selecting these groups, allowance has been made for the shift in the short and long classes as indicated by the curve shown in Figure 1. In making up the intermediate group, plants on the border line of the short or the long groups were eliminated.

Table 11.

Row. No.	No. of plants	F2 Glume Length	F3 extremes MM	Variation mm.
1723	22	9.6	8.2-19.2	11.0
1760	13	9.8	7.0-9.4	2.4
1761	16	9.8	7.6-14.3	6.7
1763	18	9.9	7.8-10.8	3.0
1768	15	8.9	8.2-10.2	2.0
1769	17	9.3	8.2-10.6	2.4
1777	32	9.9	8.2-11.2	3.0
1779	16	8.5	8.0-10.6	2.6
1780	8	9.3	8.4-10-8	2.4
1781	13	8.5	8.2-11.2	3.0
1705	8	14.1	14.4-25.8	11.4
1707	9	12.5	8.0-13.4	5.4
1708	27	12.3	7.4-18.6	11.2
1709	21	14.9	10.0-22.6	12.6
1710	9	12.5	9.2-15.8	6.6
1711	10	14.1	10.0-18.8	8.8
1712	9	13.6	9.2-23.6	14.4
1713	19	13.2	8.4-25.2	16.8
1714	13	12.7	10.2-21.8	11.6

Table 11 cont'd

Row No.	No of plants	F2 Glume Length	F3 Extremes mm	Variation mm
1716	31	13.1	8.6-21.8	13.2
1717	11	13.9	9.2-20.0	10.8
1718	29	13.5	8.0-21.8	13.8
1719	25	12.9	9.8-25.4	15.6
1724	8	13.9	9.4-21.8	12.4
1725	18	12.4	11.5-21.8	10.3
1727	12	14.5	9.0-25.6	16.6
1729	33	12.4	7.0-14.6	7.6
1743	17	14.0	8.8-20.6	11.8
1745	26	14.8	8.4-24.4	16.0
1715	25	15.1	8.4-22.2	13.8
1720	38	15.2	8.2-20.0	11.8
1728	17	17.9	7.8-25.4	17.6
1730	12	16.7	11.6-30.6	19.0
1732	9	16.6	9.0-21.6	12.6
1744	15	16.8	10.6-24.2	13.6
1746	20	17.8	13.0-22.8	9.8
1748	28	18.9	9.2-25.0	15.8
1750	32	16.3	9.2-33.4	24.2
1753	7	16.1	10.8-20.4	9.6
1755	19	18.9	8.6-22.8	14.2
1757	5	17.8	18.6-28.6	10.0
1758	6	17.4	11.0-17.6	6.6

Table 11 cont'd

Row No.	No. of plants	F2 Glume Length	F3 Extremes mm	Variation mm
1749	10	22.2	16.6-29.8	13.2
1751	31	22.7	11.8-25.8	14.0
1752	20	21.0	9.8-22.0	12.2
1754	23	25.3	18.0-28.0	10.0
1756	14	21.4	19.2-25.2	6.0
1759	4	27.3	19.4-22.2	2.8

Table 11 may be interpreted similarly to Table 10. Here again, all classes have a well determined irregularity in the inheritance of glume length. Certain rows in the short and in the long groups are possibly homozygous, but the amount of variation is sufficient to make this doubtful. It can be definitely determined only by the growing of an F4 generation.

There is a decided difference in the way the F3 groups break up. The short group segregates for short and intermediate glume length, while the long glumed group segregates for intermediate and long glumes. In the case of row 1752 there is evidence of a segregation for short, intermediate and long. However, if we compare it with row 1723, we find that the plant having the shortest glumes has longer glumes than the plant from which row 1723 was grown. This latter plant was plainly heterozygous for glume length. All rows belonging to the intermediate group were clearly heterozygous. Three kinds of segregations occur in the intermediate group; first, short, intermediate, and long; second, short, and intermediate; and third, intermediate and long.

This manner of segregation in the intermediate group, and considering the fact that no clearly defined homozygous short or long was obtained in the F2 population of 147 plants, clearly points toward a multiple factor inheritance of glume length.

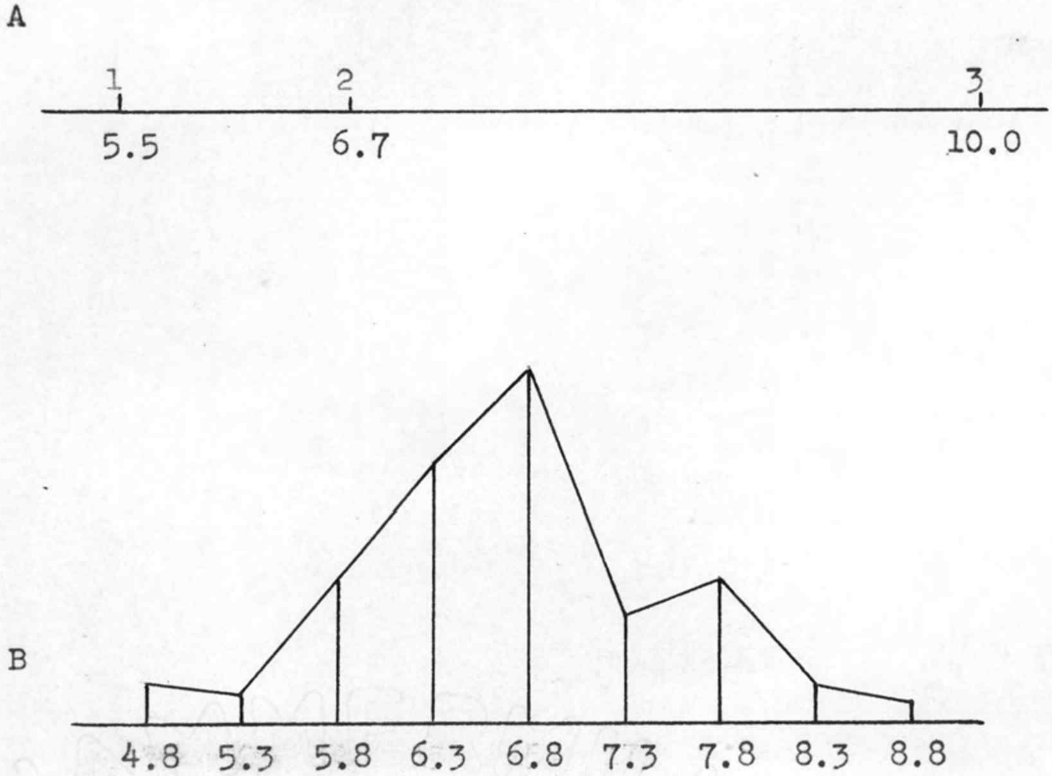
The polonicum species has longer seeds than any other species of wheat. The average seed length of the Cornwheat parent in this cross was 10 mm. The detailed data for Cornwheat parent were lost, so the extremes of seed length in this parent are not known. Marquis has a medium small, short seed. The minimum average seed length for the Marquis parent was 5.1 mm, the maximum 5.6 mm., and the average was 5.5.mm. Due to the condition of the material, only five plants of the Marquis parent could be analyzed. Had a greater number been available, a somewhat greater range in seed length might have been found. However, the head material of each parent was typical of the variety to which it belongs.

The F1 plants were intermediate for seed length, but there was evidence of a partial dominance of the short seed character as the F1 seed length fluctuated around a mean of 6.7 mm. or 1.05 mm. less than a true intermediate. The average seed length of the F1 plants ranged from 6.1mm to 7.2mm. The shape of the seed was somewhat intermediate but was a closer approach to that of Cornwheat than to that of Marquis.

The seed of the F2 plants segregated for short, intermediate, and long. They were of every gradation in length so that they could not be grouped from their appearance into these three classes. Consequently, a

Figure 2

Seed Length



A (1) Marquis seed length

(2) F1 seed length

(3) Cornwheat seed length

B F2 seed length

curve was prepared to show the number of F2 heads occuring in each of nine arbitrary classed having a range of 5 mm. in each class. Figure (2) shows this curve together with indications for the seed length of the parents, and the mean of the F1. This figure shows that there were no plants in the F2 generation with an average seed length as great as that of the Cornwheat parent, while four plants had an average seed length below the minimum average seed length of the Marquis parent. The data show a shift for the whole F2 population toward a seed length less than that to be logically expected. The lengths of the extremes and the mean are approximately 1 mm. less than the expected. Engledow (7) describes a similar shifting for both seed length and glume length in a Potish X Kubanka cross.

The time at my disposal has not permitted of a detailed examination of the F3 data in regard to the inheritance of seed length. However, the examination made shows that the rows descended from plants included in the F2 groups classed as vulgare, durum, and durum club, exhibit a greater uniformity in seed length than those rows descended from the intermediate and polonicum groups. Few rows from any group exhibited uniformity of seed length closely approaching that of the Marquis parent.

In considering the behavior of F3 rows in connection with the F2 groups from which they were descended, it might be well to call attention to the fact that the F2 plants were classified according to general appearance. Of course, the seed lengths had not been determined then.

The following table shows in a general way the behavior of the F3 generation in regard to seed length:

Table 12.

F2 Group	No. of rows.	Extreme Lengths mm	Variation mm
Intermediate	33	5.2-9.0	3.8
Polonicum	14	5.4-8.8	3.4
Vulgare	10	4.8-7.4	2.6
Durum	4	5.6-7.6	2.0
Durum Club	2	5.4-7.6	2.2

The extremes in length in the F3 generation were the same as those for the F2 generation. There was no indication of any tendency toward the recovery of the seed length of the Cornwheat parent.

INHERITANCE OF SEED COLOR

Cornwheat has seeds of a hard, horny texture and of a light amber color. But for their horny texture the seed would appear white. It is reasonably safe to conclude that they are genetically white as all hard white wheats appear somewhat darker in color than the soft white wheats. Marquis has hard seeds of a decided red color. The seeds of the F1 generation of plants (F2 seed generation) were all of a red amber color. No segregation of color accured in this generation.

In the F2 plant generation the seeds segregared into red and white. Due to sterility, only 120 of the 147 F2 plants could be classified for seed color. Of these, 104 produced red and 16 produced white seed. Reduced to its lowest terms we have the ratio 6.5: 1 With two exceptions the plants classed as white seeded in the F2 bred true for this character in the F3 generation. These two plants had seed with horny, transulucent endorsperm which is often difficult to accurately classify for color. Allowing for these two mistakes in classifying gives us an F2 ratio of 7.57 red : 1 white. Many previous crosses of Marquis with white wheat have consistently produced F2 generations that segregated in the ratio of 15 red to 1 white. Twenty-seven plants classed as red in the F2 bred true in the F3 generation. Allowing for the two mistakes in classification noted above, only 26 F2 heads produced F3 rows showing segregation of red seeded and white seeded plants. Hayes and Robertson (10) credit Marquis with two independent factors for seed color. A cross between Bluestem, a white wheat, and Cornwheat made at the Washington Experiment Station (19) failed to show any factor for red seed color in Cornwheat. The segregations taken by themselves in neither the F2 nor the F3 generations explain the inheritance of seed color on either a one or a two factor basis. In view of the fact that the seed belongs to a different generation from the plant which bears it, it might be well to call attention to the fact that seed color and seed length segregate according to the generation which bears the seed.

LINKAGE BETWEEN GLUME COLOR AND AWN COLOR

Indications of linkage between glume color and awn color were first noticed at the time the F2 data were taken. The following table shows the combinations found in the F2 generation and the frequency with which they occur.

Table 13.

Glume Color andAwn Color in the F2 Generation

Glume & Awns colored	Glumes colored: Awns White	Glumes White: Awns colored	Glumes and awns white
45	39	9	46

On the basis of single independent factors for glume color and awn color, the theoretical ratio for the above four classes is 9:3:3:1. In considering the results shown in Table 13, allowance must be made for inhibitors and the effect of environment. It is probable that some of the plants withccolored glumes and white awns carried factors for colored awns which failed to find expression.

It is also probable that the effect of inhibitors is greatest in F3 rows descended from intermediate or polonicum type plants. For this reason rows grown from the shorter glumed plants were used in making an analysis of linkage in the F3 generation. In a further attempt to avoid, as far as possible, the effect of the inhibitor of glume color, only rows grown from plants having colored glumes and colored awns have been used. Table 1r shows the behavior of these F3 rows:

Table 14.

Glume Color and Awn Color in the F3 generation.

Row No	Plants with col.glumes & Col.awns	Plants with col.glumes & white awns	Plants with white glumes & col.awns	Plants with white glumes and white awns
1760	8	0	0	3
1761	0	2	0	12
1762	10	0	0	8
1763	8	3	0	7
1766	3	0	0	2
1769	12	1	1	1
1770	1	1	0	4
1777	8	0	12	12
1779	11	1	0	4
1780	7	1	0	0
1781	7	2	1	3
	75	11	14	56

It is likely that a number of the plants having white glumes and white awns carry a factor for glume color and also the inhibitor. Probably too, some carry a factor for awn color that has failed to find expression. The F2 and F3 data furnish decided indication of linkage between glume color and awn color but the effect of the inhibitor of glume color and of environment on awn color greatly increases the difficulty of studying the relationship. Crossing over occurs, but the per cent of cases in which it takes place is difficult to determine.

GENERAL DISCUSSION

The Effects of Difference Chromosome Number in the Parents.

According to Kihara (14), the genus Triticum, to which all cultivated wheats belong, may be divided into three groups according to chromosome number: (1) The Einkorn group with seven haploid chromosomes; (2) the Emmer group with 14; and (3) the Spelt group with 21. Under this classification Cornwheat falls in the second group and Marquis in the third. Crosses between species within a group have generally proved comparatively fertile, while crosses between species of different groups produce F1 plants that are partially or, in some cases, completly sterile.

In the Cornwheat X Marquis cross under discussion, the calculated sterility of the F1 plants was 67.6 percent. In the F2 generation all degrees of sterility, from plants that were as fertile as either parent to others that were completely sterile, occured.

Cytological investigations have to some extent explained why hybrids of species of Triticum differing in their chromosome numbers are more sterile than those of similar species in which the chromosome numbers are equal. In the case of crosses between wheats of the Emmer and the Spelt groups, the one contributes 14 and the other 21 chromosomes. The resulting hybrid plant therefore has 35 chromosomes in somatic number. Kihara (14) has shown that in the reduction division of such a hybrid there are 14 bivalents. The bivalents segregate normally but the 7 univalents lag behind traveling later to the equatorial plate of the heterotypic spindle where they split longitudinally and the halves travel to the poles. In the homotypic division the univalents separate at random to opposite poles. One or more may fail to reach a pole and be left outside the daughter nucleus.

The result of this sort of reduction is that the egg cells and pollen cells contain varying numbers of chromosomes from 14 to 21. Sax (17) states that probably only those male gametes with multiples of 7 survive. Whether or not this is the correct explanation, it is well known that plants with intermediate chromosome numbers are rapidly eliminated. Cytological work in connection with this study has shown that in the F3 generation of the Cornwheat X Marquis cross most of the segregates for intermediate chromosome number had been eliminated. The great majority of F3 plants had 14 haploid chromosomes, while a very few had 21.

The effect of a condition of this kind upon Mendelian ratios is not difficult to see. If a factor for a character introduced by the Marquis parent happened to be located in one of the chromosomes pairing with those of Cornwheat, other things being equal, no interference with normal ratios would occur. On the other hand, if the factor were located in one of the group of seven which tends to be eliminated, the expected Mendelian ratior would not appear. This condition actually occurs in the cross Cornwheat X Marquis.

THE INHERITANCE OF CHARACTERS

In the work on inheritance of characters in this cross, the possible effect that differing chromosome numbers in the parents might have on normal Mendelian segregation must be taken into account. This explains why a greater use has not been made of Mendelian ratios in the data and interpretations appearing in this thesis. Account must also be taken of the action of inhibitors on two of the characters, and of the effect of environment on certain other characters.

PUBESCENCE--Biffen (2) has shown that the inheritance of pubescence in certain vulgare wheats is due to a single factor. The Howards (11) have found two independent factors to be involved in some of their crosses. Biffen (3) and Backhouse (1) have shown that certain polonicum varieties carry a factor for pubescence, the expression of which is inhibited.

Evidence has been found in the Cornwheat X Marquis, to indicate that Cornwehat probably carries multiple factors for pubescence as well as a factor inhibiting pubescence. Working upon the assumption of a single factor for pubescence and a single inhibitor, the expected ration of glabrous to pubescent in the F2 generation is 1: 1.4. This is practically the reverse of the ratio actually obtained which is 1.13 :1. The following hypothesis, while not entirely satisfactory, seems to be a far better explanation than the one advanced above: Cornwheat carries two dominant factors for pubescence PP and P'P'. To be effective, both of these factors must be present, either in the homozygous or the heterozygous condition. Cornwheat also carries the inhibitor, II. This factor when in the homozygous condition, entirely prevents the expression of the factors for pubescence. In the heterozygous condition it acts as a modifier lessening the amount of pubescence. Marquis carries recessive allellomorphs for all three factors. According to this hypotysis, the genetic formula of Cornwheat is PP, P'P', II. That of Marquis, pp,p'p',ii. Using this hypothesis, the theoretical ration of glabrous to pubescent in the F2 generation is 1.37:1.

The difference between the theoretical ration and the actual F2 ratio is wider than we would expect if the above theory offers a correct explanation of the inheritance of pubescence in Cornwheat. However, considering the conditions of the experiment, it offers a plausible explanation.

KEELED GLUMES---In this cross the sharp keels of Cornwheat are dominant over the rounded keels of Marquis. The inheritance of this character is apparently due to multiple factors. It is probably complicated by the action of modifiers as the F2 ratio of 28.4 sharp to 1 dull is far from being either a typical two factor, or a three factor ratio. No hypothesis was worked out that would account for this manner of segregation. The location of the factor for vulgare keel in one of the "vulgare group" of chromosomes could account for this type of segregation.

AWNS---The F2 generation of this cross segregared for beardless and bearded plants in the ratio of 3:1. The beardless plants were typical of the class described as "tip-awned" by the Howards (12). It is evident that Marquis carries a single factor for awns and that Cornwheat carries two. The awned segregates in the F2 generation had noticeably shorter, thicker and stiffer awns than the Cornwheat parent. In general, the long glumed plants had weaker awns that the short glumed plants. This was particularly noticable in F3 material.

GLUME COLOR---Cornwheat and Marquis both have the light straw colored glumes characteristic of white glumed wheats in general. The F1 plants have peculiar blue-black glumes. Color is undoubtedly introduced by Cornwheat, as the hybrids of Marquis with other white-glumed wheats have not shown this character. Further evidence of the source of the color is found in a Bluestem X Cornwheat cross described by the writer (19) which shows this phenomenon. Biffen (3) and Backhouse (1) have also shown that Polish Wheat carries a factor for black glumes and an inhibitor of glume color. F2 plants show a puzzling array of color; black, blue-black, brown, and red as well as the normal white characteristics of both parents. There is a decided tendency for the blue-black color to disappear in the F3 generation, and the browns and reds do not segregate according to Mendelian expectation. This behavior suggests that there is present an inherited factor or factors for but one color. According to this hypothesis, all the colored plants are genetically black. The Howards (11) and Caporn (4) have shown that the development of color, in some cases, depends partially upon environmental factors. In this case, it seems likely that the browns and reds are plants in which color is but partially developed.

Working upon the hypothesis of a single factor for glume-color and a single inhibitor gives us an expected F2 ratio of 1 white to 1.4 colored. The actual F2 segregation in this cross was 55 plants with white and 85 with colored glumes. Reducted to its lowest terms the ratio is 1:1.5. The evidence against the correctness of the hypothesis is the fact that Fl plants grown the same year under the same conditions all had blue-black glumes.

AWN COLOR---Cornwheat is classified as black awned variety altho in the parent material used in this cross the expression of this character was irregular. Some heads had black awns while others had white. In other heads there was a partial development of awn color. Observation of

Cornwheat in the field shows that this irregularity occurs between heads on the same plant as well as between plants. The fact that fully black awns are the rule shows that there is no inherited inhibitor for awn color and there is for glume color. The apical awns of Marquis wheat are sufficiently long to make color evident if a factor for it were carried by the variety. These awns are about the same color as that of the glumes.

The Howards (11) found that the inheritance of awn color in Indian wheats was due to a single factor but that its expression was controlled to some extent by environmental conditions. Considering the effect of environment, the F2 ratio of 1.25 colored to 1 white obtained in this cross seems to indicate that the inheritance of glume color in Cornwheat may be on a similar basis.

GLUME LENGTH--The F2 and F3 data indicate that the inheritance of the long glumes of Cornwheat depends upon multiple factors. From work with crosses of Triticum vulgare with T. polonicum and durum, Backhouse (1) decided that polonicum probably carries two factors for long glume, while durum carries a single factor. The 1:2:1 ratios for glume length in crosses of T. polonicum with T. tugidum and durum obtained by Biffen (2) and Engledow (7) support this theory in that they indicate a single factor difference for glume length. Comparison of heads of Triticum dicoccum with those of T. vulgare shows them to have distinctly longer glumes.

The behavior of the natural cross between T. polonicum and T. Dicoccum described by Percival (16) in which the long and the short glumed homozygotes could be readily distinguished from the intermediate heterozygotes, indicates that T. dicoccum has a factor for glume length differing from that carried by T. durum. In crosses of the latter with T. polonicum there is an over-lapping of the intermediate heterozygotes with the homozygous shorts and longs.

Taking the above facts and observations into consideration it seems probable that the inheritance of long glumes in T. polonicum is due to two independent factors. One of these is probably indentical with that carried by T. durum and the other indentical with the one carried by T. dicoccum. If this is a correct explanation, the inheritance of polonicum glumes is analogus to the inheritance of the fully awed condition as described by the Howards (12). According to this theory, hybrids of T. dicoccum and T. durum should segregate for polonicum type glumes. I have been unable to find any literature describing hybirds of this kind. Percival (16) states that he has no records of this cross. Again, he says, "Polish wheat is the most modern of all the races or sub-races of wheat, there being no evidence of its existance before the first half of the seventeenth century". This lack of any old records concerning it has caused much speculation regarding its possible origin. Due to its similarity to T. durum, it has been variously suggested that Polish wheat originated as a durum sport, and again, that it is probably the result of a cross between durum and some other wheat. As already suggested, it seems probable that Triticum polonicum originated as a cross between T. durum and T. Disoccum or the wild form T. Dicoccoides. The writer is planning crosses to test out this theory.

SEED LENGTH---The seed length of Polish wheat and vulgare wheat bear a somewhat similar relation to each other as do the corresponding glume lengths. There is some indication in the F1 of the partial dominance of a short seed character. The mean seed length of the F2 was very close to that of the F1 generation. The longest average seed length in the F2 generation was ten per cent less than the average seed length of Cornwheat. No explanation was developed that would account for the inheritance of seed length. It is probably due to multiple factors.

SEED COLOR---The inheritance of seed color will be discussed under the heading "The Relation of Characters to Certain Chromosome Groups."

This cross again exhibits what has come to be a classical example of the complete suppression of dominant characters. This refers to the factors for colored glumes and pubescence carried by Cornwheat. Biffen (3) Engledow (7) and Backhouse (1) have done considerable work on this phenomenon in Polish wheat. They have advanced theories to the effect that polonicum glume inhibits the development of color and pubescence. This has been disproved by the classification of Polish wheats published by Percival (16). This classification lists varieties with both colored glumes and pubescence. Some evidence has also been found in the Cornwheat X Marquis cross to the effect that the inhibitors of color and pubescence are closely linked with a factor for long glume altho not identical to it.

Often characters are dependent upon environmental factors for expression. The lack of favorable environment then may inhibit the expression of such a character. This condition makes much more difficult the work of understanding the hereditary factors responsible for the expression of these characters. This has effected the study of awn color in the Cornwheat X Marquis cross.

Some confusion has been caused in connection with the study of inhibitors. This is due to assuming that the sudden appearance of a character among the progeny of a cross between two parents, which themselves lacked the character, necessarily indicates an inhibitor in one of the parents. On the other hand, the appearance of segregates lacking a certain dominant character which was present in both parents, does not necessarily mean that the character has been suppressed or that the segregate lacking it is a sport.

In commenting on the suppression of characters, Biffen (3) sights an instance of two beardless wheats being crossed and producing in the F2 generation on bearded to three beardless. In light of work done by the Howards (12), the above does not necessarily constitute the suppression of a character in either of the parents, but merely the lack in each parent of one of a set of complimentary factors necessary for the expression of the fully bearded condition. If one parent carries one of these factors and the other parent has the other, it necessarily follows that bearded segregates will appear in the F2 generation. His references to the appearance of white seeded plants in the F2 of a cross of two red seeded wheats can be similarly explained. It has been shown repeatedly that the red color of seed in wheat may be due to one, two, or three factors, any of which is capable of producing color. The crossing of two red wheats, each of which carries one factor for color but differs in the factor carried, would result in segregation for red seeded and white seeded plants in the F2 generation. These cases do not in any way indicate the suppression of characters but merely the lack of expression for the want of a necessary factor.

In the case of glume color and pubescence in Polish wheat crosses, it is evident from the way segregation occurs that polonicum carries factors for both of these characters, but that their expression is inhibited by a factor or factors also carried by polonicum. This constitutes a true suppression of characters. It is possible, too, that a variety might carry an inhibitor for a given factor but unlike Cornwheat, lack the factor. The inhibitor in this case only could be demonstrated by crosses with varieties which exhibited the character in question.

LINKAGE

In the F2 and F3 generations of the Cornwheat X Marquis cross, close correlations exist between certain characters that suggest linkage. In one case linkage has been demonstrated.

Cornwheat has long glumes, and long, comparatively weak awns. Marquis has short, strong beaks. On the whole, the short glumed, awned segregates had noticeably stronger, thicker awns than the long glumed awned segregates. The few exceptions in which weak awns occured in short glumed plants suggests that they may represent cross-overs in a linkage between long glumes and weak awns. No data were taken covering this point but the condition was noticeable, especially in the F3 generation.

There is evidence of linkage between a factor determining glume length in Cornwheat and the inhibitor for pubescence. Biffen (3) and Engledow (7) have held that the long glume of itself inhibited pubescence. The occurance of short glumed F2 segregates in this cross which carried this inhibitor points to a linkage between these factors as the more probable explanation.

Linkage between factors for glume color and awn color was suspected at the time the F2 data were taken, although the condition was masked to a considerable degree by the effects of the inhibitor for glume color and of environmental factors influencing the expression of awn color. Data taken from F3 material establish the fact that linkage exists between these factors. Considerable crossing-over occurs. The exact extent has not, as yet, been determined because of the inhibitor and environmental factors referred to above.

THE RELATION OF CHARACTERS TO CHROMOSOME GROUPS

Crosses of Marquis with white wheats show Fe segregations of 15 red to 1 white. In the Cornwheat X Marquis cross the ratio is 7.57 red to 1 white. A ratio of this sort could be explained upon the assumption that Cornwheat carries an inhibitor for seed color which is effective against one of the color factors carried by Marquis but not against the other. This sort of condition gives a theoretical ratio of 8.14 red to 1 white. The above ratio is not close enough to the actual ratio of 7.57:1 to feel confident that it offers the correct explanation for the inheritance of seed color. This can be tested out by crossing Cornwheat with varieties known to carry but a single factor for red seed color. A more probably explanation is that one color factor in Marquis is carried by one of a group of chromosomes which pair with those of Cornwheat, while the other is located in one of the group which distinguishes vulgare wheat. As was explained under "The Effects of Different Chromosome Numbers in the Parents," there is a tendency in the F2 toward the elimination of this group. Upon the above basis for distribution of color factors, the total elimination of what might be termed "The vulgare group" of chromosomes would result in the ratio of 3 red to 1 white. Of course this does not occur but a sufficient number of F2 intermediates are eliminated to account for reduction from a 15:1 ratio to a 7.57:1 ratio. It is probable that this theory offers a correct explanation for the inheritance of seed color in the Cornwheat X Marquis cross.

An examination of the data on the inheritance of keel type suggests that the factor for rounded keel may also be in one of the chromosomes of the "vulgare group".

Plate 2

Abnormalities

ABNORMALITIES

Abnormalities frequently occur in species crosses of wheat, especially in crosses in which the parents have different chromosome numbers. In the F2 generation of the Cornwheat X Marquis cross there were a few plants with well developed awns on both the outer glumes and the lemmas. This condition had been previously noted in a Bluestem X Cornwheat cross (19). In the following generation, plants grown from the seed of these abnormal heads had awns on the outer glumes and many showed well developed flower parts under the outer glumes. In the case of some of the plants in the Cornwheat X Marquis cross, seeds were developed by these abnormal flowers.

Other abnormalities are shown in Plate 2. A doubling of spikelets is shown in the two outside heads. In the head on the left the double spikelets stand side by side; in the one on the right the spikelets are superimposed one upon the other. Both of these types have been described by Percival (16) and by Nilsson-Leissner (15) as occuring in crosses of Triticum vulgare and T. spelta. The second head from the left shows the double keel with two beaks on part of the glumes. The third head from the left shows the elongation of the rachillas making the characteristic head of the Poulard type. In this head there are also double, and on two joints, triple spikelets. All four heads shown in Plate2are from a single row grown from an F2 head having double spikelets. The floral glumes between the heads show an interesting case of double awns, some of them being branched part of the way while the others are separate and distinct entirely to the base.

SUMMARY

This study covers work done to date on the inheritance of eight head characters in the cross of Cornwheat X Marquis. Cornwheat belongs to the species Triticum polonicum of which the reproductive cells have 14 chromosomes. Marquis is a common variety of the species T. vulgare. The haploid chromosome number for this species is 21. The first generation of this cross was highly sterile. The second generation showed all degrees of sterility while in the third generation there was a decdied tendency toward higher fertility. Cytological work on F3 material showed that most of the segregates with intermediate chromosome numbers had been eliminated.

Both parents in this cross have white glabrous glumes. The F1 plants are characterized by glumes that show a peculiar bluish-black color and have a very fine, short pubescence. The F2 generation segregates for colored and white glumes, and pubescent and glabrous glumes. Five glume colors occur in the F2 plants; black, blue-black, red, brown and the normal white of the two parents. In the F3 generation there was only one row having plants which distinctly showed the blue-black color. The plants having red or brown glumes did not breed true for these colors.

The F1 plants have glumes a little longer than those of Marquis. Short, intermediate and long glumed plants occur in the F2 generation. The F2 segregation for glume length and F3 data indicate that long glume in Cornwheat is due to multiple factors.

There is apparently a strong dominance of the sharp keel character in this cross but its inheritance is irregular. It is probable that the factor for vulgare-type keel may be carried by one of the "vulgare group" of chromosomes.

No hypothesis was worked out to explain the mode of inheritance of the long seed character of Cornwheat. Certain similarities between segregation for seed length and segregation for glume length point to the probability of its being due to multiple factors.

Numerous crosses have shown that Marquis carries two independent factors for red seed color. Therefore, the expected F2 ratio when crossed with Cornwheat, a white seeded cariety, is 15 red to 1 white. The ratio obtained was 7.57 red to 1 white. This may be explained upon the basis of an inhibitor for seed color carried by Cornwheat, this inhibitor being effective on but one of the factors for seed color carried by Marquis. A second explanation is that one of the color factors in Marquis is located in one of the chromosomes of the "vulgare group" which tends to be eliminated in crosses with 14 chromosome wheats. The second explanation is favored as the more likely.

Several abnormalities in head structure occur in the F2 and F3 generations. These are: (1) Awns on both the outer glumes and the lemmas with the occurance of flower parts, and in some cases, seeds under the outer glumes in the F3 generation; (2) double and triple spikelets; (3) double awns; (4) double keel; (5) braching rachis. These abnormalities, with the exception of the double awns, have been shown to be hereditary. Double awns have only occured in the F3 generation. It remains to be seen if they will appear in the F4 generation.

CONCLUSIONS

Certain conclusions may be drawn from the above study. The more important are as follows:

(1) The inheritance of pubescence in this cross differs basically from any other form heretofore described. It depends upon a set of complimentary factors. The presence of very fine, almost microscopic, pubescence on certain heads in contrast to a distinct fully pubescent condition of others is attributed to the former carrying a single dose of the inhibitor of pubescence. Its partial effect in the heterozygous condition is proved by the presence of very fine faintly visible pubescence in the F1.

(2) The factor for round keel type and a single factor for seed color in Marquis are apparently located in Chromosomes belonging to the group of seven that differenciates the Spelt group of wheats from the Emmer group.

(3) Glume length and glume color are due to different factors, but these factors are linked. Considerable crossing-over occurs but the exact amount is difficult to determine, due to the action of certain modifying factors.

(4) The inheritance of the extremely long glume in Polish wheat is due to two independent factors for glume length. Either of these factors causes a slight elongation of the glumes. The rather meager data obtainable indicate that Triticum durum carries one of these factors and that

T. dicoccum carries the other, while both are present in T. polonicum. The combined action of these two factors in T. polonicum is closely analogous to the action of the two factors for tip awns, described by the Howards (12) as producing the fully awned condition.

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