INHERITANCE OF RESISTANCE TO SMUT AND OF SOME PLANT CHARACTERS IN WHEAT.

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TABLE OF CONTENTS.

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by

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INTRODUCTION

Crop improvement programs do not in all cases wait upon a knowledge of the genetics involved, but the plant breeder can proceed more rapidly and surely towards success without waste of effort when such knowledge is available. However, in many cases the successful solution of a plant breeding problem does depend on a full knowledge of the mode of inheritance of a certain character or characters Empirical methods used by early plant breeders, produced results of great value, not to be minimized in view of greater achievements attained more recently by scientific methods. But empirical methods appear to have produced already all the progress they can yield. Since the demonstration by Biffen (3) in 1903 that resistance to yellow rust, Puccinia glumarum Eriks. & Henn., is inherited in a Mendelian manner, just as are morphological characters, Mendelian principles have been applied to the problem of obtaining disease resistant crop plants. The failure of Farrer to obtain quality wheats that were resistant to black stem rust, Puccinia graminis Pers., is in striking contrast to the progress that has been made toward that

end since results of genetic studies on rust resistance and quality have been utilized by plant breeders. The satisfactory completion of this work has been delayed somewhat by a lack of knowledge on the mode of quality inheritance.

Where it is possible, without the sacrifice of yielding ability and quality to obtain disease resistant crop varieties, this would seem to be the most satisfactory method of disease control. This is true where artificial methods of control are known. The use of formalin and other chemicals for the control of bunt in wheat is general, and Jensens' modified hot water treatment for the control of loose smut is satisfactory. However, artificial control measures are not always easy to apply and always involve certain costs. In the case of smuts in wheat enormous annual losses continue, losses that, according to some writers (4,6,22,75,79), are increasing. At all times the losses from bunt in Western Canada have been considerable and such indications as were available in 1928 seemed to show that this loss was increasing, a point that has been confirmed recently by Conners (16) and others. The need of a smut resistant variety suitable to Western Canada was clearly indicated and work on the problem of producing such a variety immediately begun. The present study was undertaken to ascertain the mode of inheritance of reaction to bunt and loose smut in wheat, of certain plant characters, and to find if any relation existed between disease reaction and the other characters studied.

SMUT REACTION

Literature Review

<u>Inheritance of bunt resistance</u>.- A great deal of work has been done on the inheritance of resistance to bunt or covered smut in wheat. Most of this investigation has been carried out in Washington where the need of suitable bunt resistant varieties is greater than in regions where chemical treatments satisfactorily control the disease.

Gaines has been a pioneer in this work. Comparative bunt resistance tests on a large number of varieties in the several wheat species was followed by hybridization work with the most promising resistant strains found and varieties possessing desirable agronomic characters. He summarizes seven years work (19) in part as follows:

> "The most susceptible wheats, planted under conditions favoring maximum infection, produce an average of about 80 per cent of bunted heads. Hybrid 128 and Jones Winter Fife belong to this class. Although they produce 20 per cent of sound heads, this seems to be due to accident, for in crosses with other varieties the descendants do not show evidence of having inherited any cumulative resistance whatever from these varieties.
>
> Fortyfold, Red Russian, and Marquis each have differing dilute resistances which reduce the amount of bunt by 10 to 25 per cent. When added together, as in descendants of crosses between them, the cumulative effect makes a more concentrated resistance, having a value of 30 to 60 per cent -------
>
> ------ if Marquis is sown in the fall, only the dilute resistance is operative, for it produces but 10 to 20 per cent less bunt than the most susceptible varieties; if sown in the spring, the strong winter-sensitive factor becomes functional, and the resulting crop produces

> 60 to 75 per cent less bunt than the completely susceptible varieties. ----------
> Turkey, Florence, and Alaska each have differing concentrated resistances which reduce the amount of bunt 70 to 75 per cent, compared with the standard susceptible varieties. These concentrated resistances are also cumulative in effect when brought together in crossing, the resulting descendants segregating into immune, very resistant, various stages of dilute resistant, and completely susceptible classes".

In the Turkey X Alaska crosses the offspring showed no trace of bunt between the F_3 to F_7. Sterility and non-winter-hardiness reduced the numbers greatly in this cross and made analysis of results difficult. The Turkey X Florence cross showed transgressive segregation, the entire range from complete immunity to complete susceptibility being found. The immune segregates comprised 40 per cent of the F_3 population and it was believed they included lines that differed in intensity of resistance. Results from these and other crosses within eight varieties intensively studied seem to support the theory advanced that resistance to bunt is on a multiple-factor basis. He shows the manner in which the Turkey resistance, a b c, and the x y z resistance of Alaska might act in a cross, postulating the parents susceptibility to be 5 per cent and each factor capable of reducing the amount of bunt by 20 per cent, as follows:

Number of resistant factors	Bunt produced	Classification
0	65 per cent	Non-resistant.
1	45 " "	Slightly resistant.
2	25 " "	Somewhat resistant.
3	5 " "	Very resistant.

Number of resistant factors	Bunt produced	Classification
4	-15 (None)	Immune.
5	-35 "	Immune.
6	-55 "	Immune.

The extra resistant factors in the immune strains could only be shown up by hybridization studies. Further studies by Gaines (20) did prove that the immune wheats were more "prepotent" in transmitting resistance than wheats that show slight infection. These extended studies showed Martin, Hussar, and White Odessa to be bunt-free and hence they are considered immune. Two immune hybrids, Ridit and Selection C are mentioned.

Transgressive inheritance was reported by Gaines and Singleton (25) in a Marquis X Turkey cross. The F_2 distribution in the various infection classes supported fairly well the two-factor explanation offered for this cross. A genetic explanation of the behavior of resistance factors in this cross is complicated by the fact that Marquis is susceptible when fall sown and resistant when spring sown, while Turkey is resistant when fall sown and immune when spring sown. However it was believed the same factors governed resistance in the different seasons and this was borne out by a correlation of $+0.711 \pm 0.027$ between fall- and spring-sown rows. In these studies susceptibility was believed to be partially dominant.

Briggs (4) reviewed the work of Gaines and the earlier work of Farrer (1901) and Sutton (1910) in the production of the bunt resistant varieties Florence and Genoa by hybridization. He points out that Farrer and Sutton made no attempt to observe segregation with a view to obtaining Mendelian ratios. The same was true of Pye, another Australian worker quoted by Briggs. In his own investigations, Briggs studied crosses of susceptible x susceptible, resistant x resistant, and resistant x susceptible varieties, using Martin and Hussar as the resistant parents since they had proven completely immune from bunt. Of the completely susceptible varieties used, Hard Federation and White Federation produced about 70 per cent bunted heads and Baart about 80 per cent on the average over a five year period. Studies were made in F_1, F_2, and F_3. No resistance factors were found in the Baart X Hard Federation crosses so it was concluded that the lesser susceptibility of the Hard Federation must be due to some modifier. No susceptible segregates appeared from the Martin X Hussar cross. The other crosses showed that Martin differed from Hard Federation and from White Federation in one dominant factor for resistance, and that Hussar possibly differed from Hard Federation and from Baart in two dominant factors. One of the Hussar factors was believed to be identical with that in Martin but the effect of the other was not exactly determined.

While not proven to be a pure strain of <u>Tilletia tritici</u>, the inoculum used by Briggs in the study just reviewed (4) was obtained from a single source (Little Club) and grown from year to year on White Federation wheat. At

that time the presence of physiologic races within the *Tilletia* species was only suspected, but the value of using pure known forms of the disease organism in studying the inheritance of resistance had already been demonstrated by Aamodt (1) in studies on stem rust resistance. Recent work by Rodenhiser and Stakman (58), Reed (57), and Gaines (22) has amply demonstrated physiologic forms in *Tilletia tritici* and *Tilletia levis*.

Further study on the bunt resistant factors in Hussar wheat was undertaken by Briggs (7) and the second factor isolated in Selection 1418. This factor, which was named HH, was not completely dominant as was the MM factor present in both Hussar and Martin. In crosses between Selection 1418 and the very susceptible Little Club, the second Hussar factor allowed about 50 per cent of the heterozygous plants to become infected.

Briggs (8) has reported on the inheritance of bunt resistance in crosses of White Odessa (C. I. 4655) X White Federation. White Odessa wheat produced 2 to 3 per cent of bunted heads in inoculation tests. Study of the segregation in the various infection classes showed that these varieties differed by a single factor for resistance that behaved in a manner similar to the HH factor of Hussar. It was not determined whether the Odessa and the Hussar factor were identical. In this and the two previous studies (4,7) bunt inoculum from the same source was used.

Inheritance of loose smut resistance:- There is a dearth of literature on resistance and inheritance of resistance to loose smut of wheat, probably because no rapid and effective method of inoculating the wheat flower has been devised. The laborious method of opening and inoculating each flower by hand during the short period when infection can take place has probably proved to be the factor limiting such studies.

Olsen, et al., (53) were the first to report on inheritance of resistance to this smut. A review of this work by Matsuura (46) informs us that "there are several genes involved for resistance to smut caused by Ustilago tritici in different wheat varieties". These are said to be transmitted independently and to have a cumulative effect when they act together. No mention is made of the methods used in arriving at these conclusions.

Tisdale and Tapke (79) pointed out, as a result of inoculation studies, that highly resistant and immune strains were found in many varieties of common wheat. Fultz and Fulcaster, widely grown winter wheats, Hussar and Ridit, two hard winter varieties, and Preston, a hard red spring wheat, each contained such strains.

Later extensive tests by Tapke (75) extended this list of varieties and confirmed the observations on field resistance in certain varieties by showing these same varieties resistant following artificial hand-inoculation. On the whole the club wheats tested proved to be very

susceptible and Kota, a widely grown common wheat, was of the same order of susceptibility. Pentad, the only durum wheat tested proved highly resistant. Pure-line selections of Hussar (C. I. 4843) and Ridit (C. I. 6703) were respectively highly resistant and immune. The use of composite samples of spores, instead of spores from single heads, in the latter years of this test showed some varieties, thought to be resistant or immune, to be highly susceptible. The presence of physiologic forms of the pathogene was also indicated by this change in the reaction of certain varieties. No relation was found between hydrogen-ion concentration or titrable-acid concentration in the cell sap and reaction to loose smut in the varieties studied.

Among other things noted in a test of 6 years duration on the continued selection of large and small seed, was the increase in amount of loose smut in the plots sown to small seeds. The author, Taylor (76), suggests that this is probably the result of the presence of the loose smut organism within the developing kernel and some effect, probably on endosperm development, due to its presence and not to any hereditable factors.

A recent study, made in Germany by Piekenbroch (56), demonstrated the presence of physiologic strains in the loose smut pathogene. In crosses between certain European wheats immunity from loose smut was found to segregate in F_2 and F_3 and to be inherited recessively.

Later work by Grevel (27), another German worker, confirmed the findings of Piekenbroch, both in regard to physiologic forms and the Mendelian inheritance of resistance to loose smut on a recessive basis. Neither investigators state the number of factors involved.

Materials

Parental varieties: Three varieties of hard red spring wheat *Triticum vulgare*, Host., were used in producing the four crosses studied. All three are considered to be good yielders and fairly well adapted to central Alberta conditions.

Kota was originally introduced into North Dakota from Russia by H. L. Bolley in 1903. For a long time its merits were not recognized and it was not produced commercially until 1919. It is not a good milling and bread making wheat. Kota is a midseason variety, moderately drought-resistant and resistant to many physiologic forms of stem rust in the field. It is quite susceptible to bunt and loose smut. The middense, fusiform head is strongly awned (30-80 mm. long). Not only are there long awns on the lemmas or flowering glumes but the beak of the outer glume is elongated (3 to 20 mm.) to an awnlike point. The straw is somewhat weak and under very favorable growing conditions this variety shows a distinct tendency to lodge.

Red Bobs originated from a red-kernelled head selection made by Seager Wheeler, Rosthern, Sask., from a field of White Bobs in 1910. It was distributed commercially in 1918. This variety is a good milling wheat and its flour is nearly equal in quality to that of Marquis. Red Bobs is an early to midseason variety, not particularly drought-resistant and quite susceptible to stem rust. It is susceptible to bunt. Under the conditions of this test it proved to be immune to loose smut. The oblong, middense head is sometimes clavate, is entirely without awns or awnlets, and has beaks wanting to 0.5 mm. long. The straw of this variety is considered to be fairly strong, standing up well under most conditions.

Garnet, a comparatively recent (1926) entrant to the group of commercially important wheats, is a production of the Central Experimental Farms, Ottawa, from a Preston A X Riga M cross made by Dr. Chas. Saunders in 1905. This variety is considerably earlier than Red Bobs, and is the only high yielding variety in the very early class. It is not drought-resistant nor rust-resistant. However on account of its earliness it is rust-escaping. In this test it proved to be resistant to bunt and loose smut. The fusiform, middense head shows considerable variability in regard to the length and distribution of the awnlets. Some heads are almost bald, some bear a few short apical awnlets (2-5 mm.) only, while the majority have awnlets (2-10 mm.) well distributed down the spike. The beaks are about 1 mm. long. The straw is fine and midstrong, under some conditions showing a tendency

toward weakness. Garnet is discriminated against by millers and bakers on account of the distinctly yellow tinge in the flour it produces.

Crosses: In these studies the progeny of four crosses were used; two each of Kota X Garnet (Crosses No. 109 and No. 112) and Kota X Red Bobs (Crosses No. 115 and No. 118) The crosses were made and F_1 grown by Dr. O. S. Aamodt, at St. Paul, Minnesota, to whom the writer wishes to gratefully acknowledge his indebtedness for the F_2 material.

Source of inoculum: Studies were made of the reaction of the four crosses toward *Tilletia tritici* (Bjerk.) Wint., the spores of which were obtained from two different hosts grown at the University of Alberta in 1928. The inoculum referred to in this study as Kota bunt was obtained from bunted heads of the Kota variety. The other source of inoculum was the bunted heads of the Red Bobs variety; this material will be referred to subsequently as Red Bobs bunt.

The inoculum for the study of reaction toward loose smut, caused by *Ustilago tritici* (Pers.) Jens., was obtained from the newly emerged sporulating heads rogued from the Kota and Ceres plots grown by the Division of Plant Biochemistry of the Field Crops Department here, and a few heads from the Kota parental checks.

Methods.

General: The F_2 plants and F_3 lines were grown in spaced-plant 5-foot rows and handled on the individual plant basis. Parental checks were grown with the F_2 and at intervals of 30 rows with the F_3 and treated in the same manner as the hybrid material.

The F_3 was planted in three series. The first series was grown in the Campus field and included a row from all plants producing enough seed (25 to about 20 seeds). This was intended for the genetic and loose smut study. Where enough seed was available for two more rows, these were planted in separate series in the West field for the bunt tests. Where only enough seed was available for one additional row that row was included in the series tested with Kota bunt.

Loose smut: The F_2 material was inoculated with loose smut by making a small brush of 10 to 20 spore-bearing spikes and rubbing these against the growing heads. This was done three times at three day intervals during the time the hybrids and parental material were flowering. When each treatment was complete the spikes were covered with a brown smudge of spores. The weather during this period was clear and dry.

A minimum of five heads (from as many plants) in each F_3 line of the Kota X Garnet cross, No. 109, were inoculated by Stringfield's method (73) using loose smut from the Kota and Ceres plots, as previously, and from the hybrids themselves. This was for further study in F_4. In a preliminary test in the greenhouse this method yielded as high as 75 per cent infection.

During the shooting and filling period counts were taken of the smutted heads in all three series, and as each count was taken the smutted head was broken off at the neck. At the time the plants in the bunt tests were being examined the number of plants affected with loose smut was slso recorded. Plants smutted in the Campus series were counted at the time the material was classified for awns.

Bunt: The bunted heads from the sources already described were passed through a small hand grinder that reduced the whole to a fine powder. Care was taken to avoid contamination of each lot by spores from the other. The inoculum was applied to the seed by placing a small portion of the ground spore-bearing material in the envelope with the seed, already prepared for sowing, and shaking them well.

In the taking of bunt data counts were made in the field at harvesting time. On the pulled plants each head was carefully examined, and a plant was considered to be infected if one or more florets on any head proved to be bunted.

Experimental Results.

Bunt studies: The population of many of the F_3 lines tested for bunt reaction was reduced to a few plants by an epidemic of cutworms and a prolonged period of soil drifting in the spring of 1930. This was particularly true of lines located at the western and northern limits of the ranges containing the smut tests. However, since the distribution of the lines was essentially on a random basis in the seeding plan, a reduction in the amount of data from which to draw conclusions is the only appreciable effect of this damage. In summarizing the data from these tests all lines containing less than ten plants were discarded, the amount of infection was expressed on a percentage basis, and the lines grouped in classes according to the percentage infection. A class interval of 10 per cent was used, the infection classes described as 5, 15, 25, etc., denoting the infections within the limits of 1 to 9%, 10 to 19%, 20 to 29%, etc., respectively. A zero class was added to include all lines showing no infection.

In addition the percentage infection of the entire parental check population was computed and is shown in Table I. This was thought advisable since only two rows of the Red Bobs checks in the Red Bobs bunt series contained the minimum number of ten, required for the method of summarization just described.

Table I - Percentage smut infection of parental varieties.

Smut used	Variety		
	Kota	Red Bobs	Garnet
Kota bunt	68.3	51.2	10.4
Red Bobs bunt	30.0	36.0	2.6
Loose smut	1.5	0.0	0.6

The lower percentage of infection in all three varieties resulting from the Red Bobs bunt might be interpreted as due to a weakness in the infection capacity of that particular lot of bunt due to poor germination, lack of maturity or artificial injury to the sample, rather than to its inherent capacities. However, in view of the difference in behavior of the two lots of bunt on Kota and Red Bobs, it must be concluded that they consist of differing physiologic forms or groups of forms. The virulence of the Red Bobs bunt appears to be considerably less than that of the Kota bunt.

At the beginning of this study each cross was considered separately, but the results for like crosses proved to be so similar that it was decided to bulk the data. This decision was based, in part, on the data presented in Table II. These data may be taken to indicate, not only the identity of the duplicate crosses, but also the uniformity of the conditions of test, and bear out the assumption made in regard to the randomness of sampling in the material included for study.

Table II - Bunt segregation in F_3 lines of similar crosses.

No. of cross.	0	5	15	25	35	45	55	65	75	85	95	Total
Kota X Red Bobs with Kota bunt:												
Cross 115	--	--	--	1	3	15	28	34	32	20	10	143
Cross 118	--	--	--	5	15	22	26	33	34	8	2	145
Kota X Red Bobs with Red Bobs bunt:												
Cross 115	--	1	7	13	11	16	7	9	3	1	--	68
Cross 118	2	7	10	11	23	17	9	7	3	--	--	89
Kota X Garnet with Kota bunt:												
Cross 109	2	6	7	13	28	27	12	19	5	4	1	124
Cross 112	1	6	11	22	29	22	13	10	8	2	1	125
Kota X Garnet with Red Bobs bunt:												
Cross 109	57	32	20	7	3	1	--	1	--	--	--	121
Cross 112	30	35	23	9	9	5	2	--	--	--	--	113

(Infection classes: 0 through 95)

Since it was intended that the data should be used for comparative purposes a study was made of the distribution in the bunt classes of the lines that had a row of ten or more plants in each bunt test. This reduced number of comparable lines followed very closely the distribution of the larger total numbers in each cross so it was decided that the larger numbers be used.

Table III shows very well the heritable nature of bunt reaction. In the susceptible x susceptible crosses (Kota X Red Bobs) the hybrids occupy the entire parental infection range and no segregates more resistant than either appear. The greatest number of lines fall in the classes showing 50 to 80% infection. These results are in agreement with those obtained by Briggs (4) on the Baart X Hard Federation crosses.

Table III - Reaction of parents and F_3 hybrid lines to Kota bunt.

Parents and hybrids.	Infection classes. 0	5	15	25	35	45	55	65	75	85	95	Total
Kota	--	--	--	--	1	4	--	5	4	4	2	20
Red Bobs	--	--	--	2	--	2	3	2	--	--	--	9
Garnet	2	2	5	--	--	--	--	--	--	--	--	9
Kota X Red Bobs	--	--	--	6	18	37	54	67	66	28	12	288
Kota X Garnet	3	12	18	35	57	49	25	29	13	6	2	234

The Kota X Garnet segregation distinctly shows the introduction into the hybrids of factors resistant to Kota bunt. In discussing hybrids of which Garnet is a parent it must be remembered that the resistance of this variety is much greater than the numbers would indicate. An average bunted Garnet plant seldom showed more than one partly bunted head whereas bunted Kota and Red Bobs plants usually showed one to several, sometimes all bunted heads. A considerable number of hybrids show resistance equal to that of the Garnet parent, a larger number the high susceptibility of the Kota parent, but the greatest numbers fall in the classes showing 20 to 50% infection.

Table IV shows that the behavior of the Kota X Red Bobs hybrids toward Red Bobs bunt resembles the reaction toward Kota bunt, only the distribution is greater in the lower infection classes. The Kota X Garnet hybrids show a considerable aggregation in the non-bunted class and the two lowest infection classes. Few lines appear

showing the order of susceptibility of the Kota parent (30%), which would seem to indicate a dominance of the resistance factors.

Table IV - Reaction of parents and F_3 hybrid lines to Red Bobs bunt.

Parents and crosses	Infection classes 0	5	15	25	35	45	55	65	75	85	95	Total
Kota	--	--	6	7	2	2	3	1	--	--	--	21
Red Bobs	--	--	1	--	--	--	1	--	--	--	--	2
Garnet	6	3	--	--	--	--	--	--	--	--	--	9
Kota X Red Bobs	2	8	17	24	34	33	16	16	6	1	--	157
Kota X Garnet	87	67	43	16	12	6	2	1	--	--	--	234

Loose smut studies: Preliminary tests made in the greenhouse during the winter months of 1929-30 indicated that the percentage infection obtained from the inoculation with loose smut was very low. This was borne out later by the field studies. Only three of the lines showing infection in the Campus field series showed infection in the other two series also. In view of this condition it was decided to make no distinction between the three series, but to summarize the results on the basis of the three replicates as one. No results were taken from lines having a total population of less than ten plants.. This minimum is rather low when the average percentage of infection is considered but it should be pointed out that only a few lines had a total of less than twenty-five plants. A line was considered to be infected when one or more heads or parts of heads on any plant produced loose smut. Few lines showed more than one or two infected plants.

Table V - Loose smut infection on parents and F_3 hybrid lines.

Parents and Crosses	Total lines	No. lines infected.	% lines infected.
Kota	26	12	46.2
Red Bobs	15	0	0.0
Garnet	12	3	25.0
Kota X Red Bobs (115)	200	40	20.0
Kota X Red Bobs (118)	195	42	21.5
Kota X Garnet (109)	164	69	42.1
Kota X Garnet (112)	179	73	40.8

The close check between the similar crosses in regard to the percentage of lines showing infection is of interest in view of the low degree of infection obtained, and is further evidence that the pairs of crosses are identical in nature. The order of susceptibility in the hybrids is what one would expect from a consideration of the infection percentages in the parents as shown in Table I. No factorial explanation of the inheritance will be attempted.

SEED COLOR

Literature Review

Inheritance studies.- Since seed color is one of the most striking morphological characteristics of a wheat variety it is not surprising to find that this was one of the first characters genetically investigated in the wheat species. Numerous studies covering several varieties in all of the species groups have been made. Biffen (3) was the first to report (in 1905) on the inheritance of red kernel colour in wheat. He found red to be dominant over white in F_1 and to segregate in a 3 red: 1 white ratio in F_2.

The studies of Nilsson-Ehle (49,50,51,52) on colour inheritance in wheat established both two- and three-factor hypotheses and laid the foundation for our present conception of the inheritance of quantitative characters. It was from the cross of Svalof "Pudel" X Swedish "Sammet", two velvet-chaffed common wheats, white-and red-grained respectively, that he obtained his best results. In F_1 the grains were pale red and F_2 also gave all red, but of several shades. With a large number of lines he should have obtained a 63:1 ratio in F_2, but failed to do so from this cross. In the F_3, however, he found that some of the lines gave a 3 red : 1 white ratio, others segregated approximately

15 red : 1 white, while a few gave a segregation 63 red : 1 white.

An analysis of these results led him to postulate that the red grain colour of the "Sammet" parent was due to the presence of three dominant and independent factors R_1, R_2 and R_3, each of which by itself was capable of producing redness. He explained the varying shades of red obtained as due to "additive or cumulative action of the several colour factors", the presence of two or three factors giving twice or thrice the depth of colour that one factor would produce. Only when the three factor pairs were homozygous for red would the original dark red of the red parent be recovered; the whites would all breed true since they must be homozygous recessive ($r_1r_1r_2r_2r_3r_3$); and between these extremes would be five shades of red.

On this hypothesis the genotype of the red parent would be $R_1R_1R_2R_2R_3R_3$, while that of the white would be as for the homozygous recessive just given. From the F_1, which would have a constitution of $R_1r_1R_2r_2R_3r_3$ we should get the theoretical proportions of 64 individuals having 27 different genotypes. These are shown in the accompanying Table VI. The genotypes are arranged in descending order of the number of single R genes of the F_2 genotype. The theoretical F_3 breeding behaviour is also shown with the proportions in each breeding group given in percentages. This will be referred to later when the work of Gaines (18) is being discussed.

Table VI-Segregation for Red Colour in Wheat - Based on the Three-factor Hypothesis.

No. in each class	F_2 Genotype			F_2 Colour	No.	F_3 Colour and theoretical Segregation	%		Obtained by Gaines (18 %
1	RR	R'R'	R''R''	D		D	1.6		17.2
2	RR	R'R'	R''r''	D		M_x			
2	RR	R'r'	R''R''	D		M_x	9.4		
2	Rr	R'R'	R''R''	D		M_x			
1	RR	R'R'	r''r''	M		M			
1	RR	r'r'	R''R''	M		M	4.7		9.6
1	rr	R'R'	R''R''	M		M			
4	RR	R'r'	R''r''	D		M_x		46.9	23.2
4	Rr	R'R'	R''r''	D	37	M_x			
4	Rr	R'r'	R''R''	D		M_x			
2	RR	R'r'	r''r''	M		M_x			
2	RR	r'r'	R''r''	M		M_x	37.5		
2	Rr	r'r'	R''R''	M		M_x			
2	Rr	R'R'	r''r''	M		M_x			
2	rr	R'R'	R''r''	M		M_x			
2	rr	R'r'	R''R''	M		M_x			
8	Rr	R'r'	R''r''	D	8	63R:1W		12.5	10.7
1	RR	r'r'	r''r''	L		L			
1	rr	R'R'	r''r''	L		L		4.7	10.0
1	rr	r'r'	R''R''	L		L			
4	Rr	R'r'	r''r''	M		15R:1W			
4	Rr	r'r'	R''r''	M	12	15R:1W		18.7	17.2
4	rr	R'r'	R''r''	M		15R:1W			
2	Rr	r'r'	r''r''	L		3R:1W			
2	rr	R'r'	r''r''	L	6	3R:1W		9.4	10.0
2	rr	r'r'	R''r''	L		3R:1W			
1	rr	r'r'	r''r''	W	1	W		1.6	2.1

Total Bulked F_3 94.1%R : 5.9%W

Legend:

D = dark red M_x = mixed red W = white

M = medium red L = light red

The segregation in F_3 of the sixty-four possible F_2 individuals should give an indication of the number of heterozygous factors present. The segregation from individuals having 4 or more factors, however, can only be estimated from the intensity of colour. This is an almost impossible thing to do. Those showing red and white must therefore be relied upon to give the necessary information. The behaviour of an F_2 tested by Nilsson-Ehle in F_3 gave a very close agreement with the expected figures as shown below.

Table VII - F_3 segregation of F_2 plants having a given number of heterozygous factors for color. Numbers given are proportional.

Number of Heterozygous factors present, F_2	4 or more	3	2	1	None
Segregation for red : white in F_3	Constant red	63:1	15:1	3:1	Constant white
Number of individuals (Obtained)	37	8	12:3	6:6	1
Number of individuals (Theoretical)	37	8	12	6	1

He showed that red color was due to three factors in "Grenadier" as well as in "Sammet". In addition, work with "Extra Squarehead 11", "Bore" wheat, and a pure line of Swedish <u>T. compactum</u>, proved them to be two-factor reds. Hybrids of these three varieties with a white-grained wheat segregated in F_2 in a 15 red : 1 white ratio. In a red x red

cross, using "Bore" wheat x "Extra Squarehead", Nilsson-Ehle (52) reoords the occurrence of white-grained plants in F_2. His suggestion that two independent and different factors for red (R_1 and R_2) are concerned, the respective uniting gametes being R_1r_2 and r_1R_2 does not check with the results reported for these varieties when they were crossed with white-grained wheats. The two-factor hypothesis for each could not be maintained and get a ratio of 15 red : 1 white in the F_2. If Percival's (55) review of the work is exact, one explanation of these results is that the parents must have been heterozygous for one of the red factors as well as each possessing one colour factor differing from the other's. This would permit finding white-grained plants in F_2 but not in a 15:1 ratio with red.

Before leaving the work of Nilsson-Ehle it should be mentioned that he found the gene R for red seed colour to affect both the structure of the testa and the power of germination (52).

Howard and Howard (39,40), working about the same time as Nilsson-Ehle, published in 1912 and 1915 evidence of a similar nature showing the existence of two factors for red in some Indian varieties of _T. vulgare_, and the presence of three factors for red in a _T. compactum_ known as "American Club".

In a series of crosses in Washington, 1917, between several club varieties and several common wheats, Gaines (18) confirmed the two- and three-factor hypothesis of Nilsson-Ehle. In analysing his results he used only three red

colour classes. He assumes that each R produces the same colour of red whether heterozygous or homozygous, and that the effect of the different factors R, R' and R'' is cumulative. These assumptions differ but little from those of Nilsson-Ehle, and he admits that there may be more than three colour classes. Difficulty in distinguishing between these shades seems to be great. Even with the modified grouping he does not make a very exact subdivision of the classes on breeding behaviour (See Table VI). However, when the breeding classes are grouped he gets a fairly good fit.

Table VIII-Observed and calculated segregation in F_3 in some crosses of wheat (Gaines,18). Summary from Table VI.

Total F_3 families (expected breeding)	37 Red : 26R + W : 1 White
" " (percentage)	57.9%R : 40.5%R + W : 1.6%W
Segregation obtained in F_3	60.0%R : 37.9%R + W : 2.1%W

On the whole, Gaines' results support the assumption of three independent factors working together to produce the red and white colour phenomena in wheats. However, he points out that it is not sufficient to explain all the colour inheritance results found. He reports two cases in which red seed was produced from a white x white cross. This would indicate that another factor or set of factors was concerned. These would probably be inhibitory in effect.

Percival states (55) that the usual result of crossing two white-grained wheats is the production of white-grained plants only in subsequent generations. He reports, however, that two workers found otherwise. Vilmorin obtained red-grained plants in the F_2 of a _T. polonicum_ x _T. turgidum_ cross both parents being white-grained. Pitsch crossed "Squarehead" and "Challenge", two white-grained wheats, and obtained a few reddish-grained plants in F_6. These results, with the few discrepancies already mentioned in some of Nilsson-Ehle's work, lend support to the possibility of some inhibitory factor operating in colour inheritance.

Love and Craig (44) in connection with their study of wild wheat forms report that the ratios obtained indicate that two factors are concerned with red colour in _Triticum dicoccum dicoccoides_, the wild wheat of Palestine. Studies, reported in their second paper (45) on crossed between Kubanka (white) and both the "synthetic wild" and true wild show similar inheritance in each and confirm the two-factor hypothesis set forth in the first paper.

Harrington (28) studied some of our common wheats and concluded that Kitchener contained two independently inherited factors for red grain colour. In some strains of Red Bobs and Hard Red Calcutta he found two factors, in others one. This probably indicates that these two varieties are made up of red strains that are indistinguishable, one of which has a single factor pair while the other has two pairs for red. Awning and seed color were studied in these crosses but were found to be independently inherited.

Harrington and Aamodt (31) found no relation between seed colour and resistance to Puccinia graminis tritici but report a 3:1 ratio for red and white colour in the F_2 of the durum crosses they studied. The crosses used were Kubanka No. 8 and Mindum by Pentad, the latter being the red-seeded parent. Pentad evidently carries a single factor for red.

Clark (10) reports on several reciprocal crosses between Hard Federation and Kota. He obtained a fairly good agreement to a two-factor or 15:1 ratio. When Kota (red-kerneled) was used as the female parent a much better fit was obtained than when the reciprocal cross was made. He suggests a possible slight maternal influence.

Hayes and Robertson (38) worked with crosses of Bobs (white), Minturki and Kanred (red winters) with Marquis (red). The Marquis x Bobs crosses, made reciprocally, gave a 15:1 ratio indicating that Marquis carries two independent factors for red. The red x red crosses gave a 63:1 ratio for red and white in F_2. The results were explained on the basis of two factors for red in Marquis and a single but different factor in Minturki and Kanred. The constitution of Marquis is given as RRR'R'r''r''; and that of the two winter wheats, rrr'r'R''R''. In one cross the "Marquis" parent turned out to be Red Fife and, since no disturbance of the expected ratio occurred, it may be surmised that Red Fife has a complement of colour factors similar to that of Marquis.

Clark and Hooker (13), like all former workers found red to be dominant over white. They used reciprocal crosses of Marquis and Hard Federation, a white-grained wheat, and, in 10 families out of 12 studied, obtained a very good fit for a 15:1 ratio, indicating that two factors are concerned with red kernel colour in Marquis. The two other families gave a satisfactory fit for a 3:1 ratio indicating that a single factor only was concerned. This difference in the ratios obtained indicates, according to Clark and Hooker, that either Marquis does not have homozygous dominant factors for red-kernel colour, or the Hard Federation parents differed in their genotype. It seems that heterozygous Marquis would be the more satisfactory explanation. This same condition was postulated by Harrington when he found one and two factors for red in lines of Red Bobs and Hard Red Calcutta.

In a cross between pure lines of Kanred and Sevier 59, red- and white-grained respectively, Stewart (69) has recently obtained segregation on a three-factor basis. Correction of the F_2 analysis was made in F_3 and although an excess of true-breeding reds and a deficiency in the segregating classes was found this was explained by the fact that only 30 to 40 plants in each progeny were available. These numbers were not thought sufficiently large to show the one plant with white grain where a 63:1 segregation was expected. In spite of this a very good fit was found, as indicated by a value of P = 0.4060. Although these results are not in accord with those of Hayes and Robertson (38), who found only one factor for red in Kanred, Stewart offers no comment on the matter.

Stewart and Tingey (72) found duplicate factors for red color in the cross Marquis X Federation (white-grained). The closeness of fit between the observed and the theoretical segregation in F_3 on a 7:4:4:1 basis is indicated by the value of $P = 0.6155$. An attempt was made to correlate glume and seed color factors but these were found to be independently inherited.

Segregation for color was studied by Stewart and Price (71) in a cross between pure lines of Sevier and Odessa, a light red-kernelled variety. They concluded that a one-factor difference was responsible for color segregation in this cross although a very poor fit was obtained for the expected 1 homozygous red : 2 heterozygous : 1 homozygous white ratio. The excess in the heterozygous class was about equal to the deficiency in the homozygous white class. However, the material was grown on land seeded to Kanred the year previously and the possibility of volunteer red wheat in the homozygous class is suggested as a probable cause of the discrepancy.

Results of other investigators, whose papers are unavailable, must be omitted from this review, Among the most important of these are Malinowski (1914), Mayer-Gmelin (1917), Kajanus (1918, 1923), Lathouwers (1924), Meyer (1925), and Vavilov and Jakushkina (1925). Matsuura (46) reports them as finding mono-,di- and trigenic ratios in their work on various species and varieties.

Triploid factors and chromosome number.- Gaines (21) has pointed out an interesting feature in connection with the heritability of quantitative characters, such as we have been discussing, and the theory that the chromosome complement of the wheat and oat species is made up of three groups of seven each. The work of Sakamura (59) in wheat and of Kihara (42) on the chromosomes of oats showed that in these genera were species having the haploid numbers 7, 14 and 21, the most valuable commercial varieties of each being found in the 21-chromosome group. This work was confirmed by Aase and Powers (2), and numerous other workers. The eight important *Triticum* species were grouped as follows by Sakamura in 1918.

T. vulgare	42 diploid	Vulgare group
T. compactum	42 "	
T. spelta	42 "	
T. turgidum	28 diploid	Emmer group
T. durum	28 "	
T. polonicum	28 "	
T. dicoccum	28 "	
T. monococcum	14 diploid	Einkorn group

It is interesting to note at this point that 1,2, and 3 duplicate factors were found in the crosses just reported in the *vulgare* group of wheats. Where the parents were from the emmer group (44,45,31), only one and two factors could be found. A short summary of the number of factors found in the varieties studied is given below.

Authority	Varieties	No. of factors for red
Nilsson-Ehle	Sammet, Grenadier	3
Nillsson-Ehle	Squarehead 11, Bore, Swedish *compactum*	2
Howard and Howard	American Club	3
Gaines	Goldendale Bluestem Minnesota Bluestem 169 Turkey x Bluestem Wash. 538	3
Harrington	Kitchener	2
Harrington	Red Bobs, Hard Red Calcutta	2 and 1
Clark	Kota	2
Hayes and Robertson	Marquis, Red Fife	2
Hayes and Robertson	Minturki, Kanred	1
Stewart	Kanred	3
Stewart and Price	Odessa	1
Stewart and Tingey	Marquis	2
Clark and Hooker	Marquis	2 and 1
Love and Craig	*T. dicoccum dicoccoides*	2
Harrington and Aamodt	Mindum, Pentad	1

In other characters than colour of kernel we find three duplicate factors. In work reviewed in another section we find that Gaines (19,20) noted the cumulative effect of three factors for resistance to bunt in the crosses made and tested in Washington between three resistent varieties (Turkey, Florence, Alaska) and the susceptible varieties (Jenkin, Hybrid 128, Jones Fife). Owing to the difficulty of obtaining smut infection, a completely susceptible variety was considered to be one showing around 80% bunted heads under the optimum conditions for infection. The most logical

explanation found to fit the frequencies obtained in the infection classes, and also the breeding behaviour of the segregates tested, was the cumulative three-factor hypothesis.

Harrington and Smith (32,63) have obtained a three-factor difference in their studies on wheat albinos. This is a very clear-cut character and lethal in action, since the homozygous recessive plant has no chlorophyll and must die when the endosperm supply of food is exhausted. They (32) used a cross of Khapli and Early Emmer, two varieties of T. dicoccum (14 haploid). Results showed two recessive genes for the inhibition of chlorophyll development present in both Khapli and Early Emmer. In F_3 some progenies consisted of green seedlings only, others gave a segregation in ratios approximating 3:1 and 15:1 for green and yellow seedlings. Later work (63) was with a Marquis and Vernal cross. Vernal is a T. dicoccum wheat (14 haploid) and was shown to carry two recessive genes for albinism while Marquis (21 haploid) carried a third, different from those of the Vernal. In F_3 some progenies gave green seedlings only, while some segregated for green and yellow seedlings in ratios approximately 3:1, 15:1 and 63:1.

Theoretically when we have a three,independent, duplicate factor difference in a cross we should get seven different genotypes in the F_2 which in F_3 breed as follows: three should remain homozygous for the dominant character, one should remain homozygous for the recessive character,

and three should segregate in 3:1, 15:1 and 63:1 ratios. Obviously, where a recessive lethal is concerned, the homozygous recessive line cannot be found in F_3. The given numbers are not the proportionate ones in each line, but merely indicate the different kinds of lines that are found - a glance at Table VI shows the different proportions to be expected in seed color, a typical case of triploid factor inheritance, to be 37 (true red) : 8 (63R : 1W) : 12 (15R : 1W) : 6 (3R : 1W) : 1 (pure white).

The presence of three sets of seven haploid chromosomes in our common or vulgare wheats is generally conceded. Whether or not these are duplicate sets is not surely known. In all probability two sets are alike and the third very similar. Percival (55) holds that the common wheats, or 21-chromosome (haploid) wheats, are of hybrid origin from natural crosses of the emmer wheats and two Aegilops species, Aegilops cylindrica and A.ovata, 14 chromosomes being contributed by the emmer parent and 7 by the Aegilops (the other 7 of the Aegilops being lost in reduction division, or as a result of the sterility of certain types of gametes and zygotes formed). His hypothesis, based on genetical and cytological, as well as morphological evidence, is borne out by extensive cytological investigations of Sax (60,62), Thompson (77,78), Aase and Powers (2), Gaines and Aase (23), and others.

Where such characters as we have mentioned, red and white colour of grain, resistance and susceptibility to bunt, and presence and absence of chlorophyll are common to both races we might expect to find three duplicate factors

governing their appearance in certain crosses. There is nothing, however, to indicate that other secondary factors of a complementary or inhibitory nature might not be present, either singly or in series. The supposed hybrid origin of wheat makes possible the assumption that either one or two sets of such factors might have been introduced by one parent and that no similar factors were contributed by the other parent. It has been already suggested that a set of inhibitors of the red factors might account for the appearance of red-kernelled segregates from the white x white cross reported by Gaines (18). If a trigenic set of inhibitors were present, operative only against a single R factor, it could cause the production of a white (masked red) individual in 1 out of 2048 cases where three factors for red were concerned. This would disturb ratios very little and might pass unnoticed for a long time. However, the parallel noted in the three factor hypothesis for certain characters and the chromosome grouping in wheat species is of considerable interest. It occurs in oats and has been proven for several characters, but no review will be made of that work here. The cultivated oats also belong to the 21 haploid group, in the genus Avena.

Gaines (21) states that each of the three chromosomes that carry the factors apparently stays within its own group of seven, but this can hardly be considered as true since there are numerous examples of the successful transfer of characters from one species group to another in interspecific crosses (61,66,77,78,81).

One further proof of the reduplication of factors for a given character is seen in the work of Stadler (64,65) on induced mutations with X-rays. He has obtained many mutations when his treatments were applied to barley, which contains only one set of 7 chromosomes in our commonly cultivated species. Most of the induced mutations were chlorophyll deficiencies and appeared fairly infrequently in the progeny of the treated oats and wheat. He gives the induced mutation rate in *Hordeum vulgare* as 4.9×10^{-6} per r-unit of radiation intensity (64), and ascribes the lower frequency of induced mutation in *Avena sativa*, *A. byzantina* and *T. vulgare* to "gene reduplication in the polyploid species". In *A. brevis*, *A. strigosa* and *T. monococcum*, 7 haploid chromosome species, the mutation rate was comparable to that of the 7 chromosome *H. vulgare*. The rate was found to be distinctly lower in the 14-chromosome wheats, *T. durum* and *T. dicoccum*, than in *T. monococcum* (65).

Materials and Methods.

The source of the material and the method of growing and handling it in the field has already been described in the section on smut reaction.

The Kota X Red Bobs crosses (Nos. 115 and 118) only were studied for seed color, since no segregation for this character took place in the Kota X Garnet crosses. The seed from the F_2 plants was classified as either red or white. In F_3 twenty-five plants were taken on which to determine color segregation in each line. Since there was seldom the full twenty-five plants from the Campus series rows the deficiency was supplied by plants taken at random from the bunt-free population of replicates in the Kota smut and Red Bobs smut series. Seed color determinations were made as in F_2 by ocular examination.

Experimental Results.

The segregation for seed color noted in the Kota X Red Bobs F_2 hybrids clearly indicated that two factors were concerned in this cross. Table IX shows the F_2 results. The odds of 1.31:1 indicate a very good fit.

Table IX - Segregation in F_2 for seed color in Kota X Red Bobs crosses.

Color Class	Number		Dev.	P.E.	D/P.E.	Odds
	Observed	Calculated				
Red	376	372.2	3.8	3.25	1.16	1.31:1
White	21	24.8				

Probable errors for numbers of individuals given here and elsewhere in this paper were obtained from tables of probable errors of Mendelian ratios, prepared by the Department of Plant Breeding, Cornell University, Ithaca, N.Y.

In F_3, a population segregating on a 15 red : 1 white basis in F_2, is expected to give a 7:4:4:1 ratio. That this expectation was not fulfilled in this case is shown by Table X.

Table X - Segregation in F_3 for seed color in Kota X Red Bobs hybrids.

Color Class	Expected Ratio	Number		O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
		Observed	Calculated			
Red	7	324	168.9	155.1	24056.0	142.43
15R:1W	4	15	96.5	81.5	6642.3	68.83
3R:1W	4	26	96.5	70.5	4970.3	51.51
White	1	21	24.1	3.1	9.6	0.40

P = extremely small $\chi^2 = 263.17$

The fit is extremely poor for the segregating classes and the true-breeding red class. The discrepancy may be due to the small numbers used to test segregation in F_3. Twenty-five plants in each line were used in most cases for this purpose and it is believed that many lines in the red class would have shown segregation if larger numbers had been used. This explanation may hold in regard to the lines that should have shown segregation on a 15:1 basis but does not appear so valid for the 3:1 group.

AWNS

Literature Review

Inheritance studies: The early work on the inheritance of awns or beards in wheat is well summarized by Percival (55). He points out that the F_1 progeny and subsequent generations from a cross between two fully awned forms were always fully awned if the parents were of the same race. If the parents were from different races the F_1 was usually awned, but frequently segregation for awnless and intermediate types occurred in F_2 and later generations. He cites the work of Vilmorin, who obtained an awnless _vulgare_ form from descendants of a cross between awned varieties of _T. polonicum_ and _T. turgidum_.

Investigations on crosses between awned and awnless forms were numerous and yielded conflicting results. This is understandable since the awnless classes included forms having short tip awns (.3 to 1 cm.). In crosses within species the awnless character was considered dominant. This view was modified by Saunders to one of incomplete dominance. He pointed out that intermediate F_1 types often occurred. A majority of the crosses between "short-tipped" awnless and fully awned gave a 3 awnless dominant to 1 awned recessive in F_2. In such crosses "semi-bearded heterozygotes" were noted. Differing little from those homozygous for short awns they had been grouped

as awnless by the earlier workers. Howard and Howard (39,40) studied several crosses between awned and true-awnless _T. vulgare_ varieties. The F_1 had apical awnlets and the F_2 segregated on a two factor basis, giving a ratio of 15:1 between the grouped forms with any length of awns and the true awnless. They classified the plants into five groups and explained their results on the basis of two factors, B and T, producing long and short awns respectively, both necessary to the production of fully awned plants. An exception to the general results of other investigators was found by Tschermak. The awned character was not recovered in the descendants of two different crosses involving awned and awnless varieties. Saunders pointed out that the character of the awns in the F_1 varied with the wheats used in the various crosses, and questioned the single factor hypothesis.

In crosses between two "beardless" forms the usual result was the production of "beardless" both in F_1, and subsequent generations. However, according to Percival, Rimpau and Spillman each obtained constant awned forms from such crosses. The Howards (40) crossed some of their "long-tipped" awnless (BBtt) and "short-tipped" (bbTT) forms and obtained some fully awned lines in the F_2.

Some early work not mentioned by Percival was done on this continent by Kezer and Boyack (41) and Gaines (18). Gaines studied several crosses between long-headed awned and club-headed awnless varieties. Length of

head and awn characters were found to be inherited independently, each on a simple 1:2:1 basis. The "awned" factor was partially dominant and no stable intermediate forms were found. The different types were readily classified in these crosses and it was noted that the factor for shortening the length of the rachis also shortened the length of the awn on the club heads. Kezer and Boyack believed awnlessness to be partially dominant. They used Turkey Red as the awned parent and two apically awnletted varieties, Fultz Mediterranean and Harvest King, as the awnless parents in their crosses. They classified the intermediate segregates as awnless and reported one-third of the awnless class to breed true in F_3 from a 3 awnless : 1 awned segregation in F_2.

Harrington (28) studied crosses of Red Bobs (bald) X Taylor's Wonder (tip-awned), Hard Red Calcutta (awned) X Taylor's Wonder, and Hard Red Calcutta X White Bobs (bald). He obtained a 3 tip-awned : 1 bald ratio in F_2 from the bald X tip-awned cross, making no attempt to separate the intermediate tip-awned (heterozygous) forms from the fully tip-awned. The cross between the awned and tip-awned also gave a single-factor difference ratio, no attempt being made to separate in this case the homozygous and heterozygous tip-awned classes. The awned X bald cross in F_2 presented many difficulties in classification but a very close agreement was found between the observed and expected two-factor results. The results of these crosses were in agreement with those of the Howards. Harrington used their factorial explanation for

the genotypes of his parents and the subsequent segregation of forms.

Among other characters Clark (10) studied awning in the progeny of several reciprocal crosses between Kota and Hard Federation. Kota is a strongly awned spring wheat while Hard Federation is bald or true awnless. In analysing his results from the Hard Red Calcutta X White Bobs cross Harrington had used five awn classes, giving them descriptive names similar to those of Howard and Howard but he published no detailed description of them. The classification of types of awning as described by Clark (10) is now used by most investigators in America. Five classes are made, described as follows:

> " (1) awnless, (2) apically-awnletted (3) awnletted, (4) short-awned, and (5) awned. Class 1, awnless, normally is entirely without awnlets in the apical part of the spike, although a few awnlets 1 to 2 mm. long may occur at the apex under abnormal conditions. Class 2, apically-awnletted, has awnlets 2 to 20 mm. long at the apex of the spike but rarely extending to the central or basal portions. Class 3, awnletted, has awnlets from 3 to 4 mm. long, the shorter occurring at the base of the spike and the length increasing toward the apex. Class 4, short awned, has short awns throughout, varying from 15 to 50 mm. long but only about half the length of the normal awns. In Class 5, awned, the awns vary from 30 to 80 mm. in length".

Clark found that these classes were fairly definite and that any doubt regarding classification could be cleared up by studying the breeding behavior in F_3. The F_1 plants were classified as apically-awnletted in these crosses. By grouping his results on the populations grown at three

stations he obtained a 3 : 1 ratio between classes 1, 2 and 3 and classes 4 and 5. However, by analysis of the five groups separately in F_3 he obtained a fairly close fit for a two factor hypothesis. He also concludes that the belief of Howard and Howard as to the recessiveness of the awnless character is not applicable to this cross. For the Kota X Hard Federation crosses two factors must be present in the dominant condition to produce awnlessness while at least double recessive factors are required for the fully awned condition. Complete homozygosity in the groups 1 and 5 could only be explained on a multiple factor basis, the two major factors, which he considers to be equal in effect, not being sufficient to account for the results obtained. Gaines and Singleton (25) report on awning in crosses of Marquis and the fully awned winter wheat, Turkey Red. They obtained a 3 awnless : 1 awned ratio. They considered only the fully awned as awned and grouped awnless and intermediate forms in the awnless class. The fit obtained however was not very good, the ratio 2.5 : 1 in F_2 not being considered satisfactory. In spite of this the fact that the awned all bred true in F_3 was taken to indicate that awns were inherited as a unit character. A table is presented by these authors showing that the percentage awned in other crosses of Turkey with the awnless varieties Fortyfold, Triplet, Ruddy, Hybrid 128, White Fife, and Jenkin, closely approaches the expected 25% required on a single factor basis.

Gaines and Carstens (24) report a case of linkage between the factors b for awns and V for pubescent node in a cross between the awnless club wheat, Hybrid 128, and Velvet Node, a bearded, common wheat with a pubescent node. In this cross the segregation in F_2 for awns is on a single factor basis, so a 9:3:3:1 ratio would be expected if the inheritance of these characters was independent. The results approached a 2:1:1 ratio and only 2 awned plants with glabrous nodes appeared instead of the expected 24 in a population of 393. About 5 per cent crossing over occurs, indicating a strong linkage.

A cross between a pure line of Federation and Sevier 60 was studied intensively by Stewart (67). Four true-breeding awn classes were obtained, one for each parental type and two intermediate forms. They were: class 1, awnless, like the Federation parent or almost so; class 2, short-tip awns; class 3, short-tip awns in lower half of spike and part-length awns in upper half; and class 4, fully awned, like the Sevier parent. The F_1 plants belonged in awn class 2. In F_2 the variation made classification in classes 2 and 3 very difficult. There was an indication that two factors were responsible for the segregation obtained. All families (F_3) showed a preponderance of numbers in the true-breeding parental classes, suggesting a linkage; and it was concluded that the data on this cross was best explained by the presence of two factors A and T for awns located on the same chromosome with crossing over to the extent of about 35 per cent. A small,

but apparently significant correlation was found between spike density and awn class. This author draws attention to the linkage of awns with spelt and with speltoid forms in _spelt_ X _vulgare_ crosses found by Nilsson-Leissner (1925) and by Meyers (1925).

Stewart (68) undertook further studied on Sevier crosses in an attempt to test the conclusions reached in 1926 (67). For this purpose two crosses on pure line Federation were used. One was with a pure line of Sevier, different from Sevier 60, and designated No. 59. The other was with a segregate from the cross Sevier X Dicklow known as G-149. Both are fully awned. The same difficulty as formerly reported was found in classifying the intermediate forms in F_2. However, study of the breeding behavior in F_3 made for accuracy and the method of classification was considered adequate by Stewart. The data obtained confirmed the linked two-factor hypothesis with 35% crossing-over. Both crosses showed a very excellent fit to the numbers expected, and while absolute proof of linkage was not obtained the original theory was considered to be approximately correct. Each factor was found to produce when separate effects that could be readily identified in the progenies concerned.

In the paper just reviewed (68) the author points out that Nilsson-Ehle (1920) obtained by mutation true-breeding forms of awnless, half-awned, and awned wheats. A partial dominance of the awnless and half-awned forms over the more awned types was noted. The results obtained were explained "on the basis of multiple allelomorphs for half-awned and fully awned plants arising by complex mutation from the awnless plants."

Clark and Hooker (13) worked with Marquis X Hard Federation, representing crosses of awnletted X true awnless. They obtained only three kinds of awns in F_2 falling in classes 1, 2 and 3. For these classes they obtained a 1:11:4 ratio in F_3, and believed that in the primary pair the awnletted allelomorph was recessive while in the other or secondary pair the awnless factor was recessive. A close fit is indicated by the value of $P = 0.896$ obtained.

Clark, Florell and Hooker (12) working at Davis, California, used Bobs and Hard Federation as the awnless parents and Propo as the awned. In the F_2 the grouping of the classes 1 and 2, against 3, 4 and 5, gave a 9:7 ratio, suggesting that the principle segregation was due to a two factor difference. This 9:7 ratio was found to consist of a 1:8:4:2:1 phenotypic ratio suggesting two major factors with unlike effects in the Bobs x Propo cross. In the Hard Federation x Propo cross the breeding behavior in the F_3 gave a 1:35:16:8:4 ratio with a very close fit. This 3 factor ratio was considered to be the result of two major and one minor factors. The two awnless parents were crossed (i.e. Bobs X Hard Federation) giving a segregation into classes 1 and 2 on a 13:3 ratio. This was explained on the basis of two minor factors and served to clear up some difficulties in the Propo crosses into which they entered. Summarizing the inheritance of awnedness in these three crosses they conclude that the Bobs X Propo cross may be represented by the formula AABB X aabb;

the Bobs X Hard Federation by AABBccDD X AABBCCdd and the more complicated Hard Federation X Propo cross by AABBCC X aabbcc. The AA factor is supposed to have a greater effect than the BB factor in reducing awnedness. They are considered to be of major importance but only possess imcomplete dominance for awnlessness. The CC and DD factors are considered to be minor factors equal in degree of effect but CC intermediate and DD dominant in effect. Considering these, and the Kota X Hard Federation crosses reported on previously (10), they conclude that as many as four factors may be involved in inheritance of awnedness in some wheat crosses. This presents a much more complicated picture than the single factor explanation found by earlier investigators.

In crosses between Kanred and Sevier 59, two fully awned wheats the segregation noted by Stewart (69) was such that no genetic interpretation could be made. The awns of Sevier 59 are considerably shorter than those of Kanred and the head, though not a club, is more dense. That there is a linkage between spike density factors and awn length seems beyond doubt. The values of r were always "+" and high, indicating that the longer spikes had longer awns.

A study was made by Stewart and Tingey (72) of awning in a Marquis X Federation cross. According to the Stewart classification (67) both parents fall in class 1, nearly awnless. In F_3 the lines from this cross were separated into homozygous class 1, homozygous class 2, in which the awns were short but distinct, and a third group segregating for both classes. A single factor of

major importance was considered to be responsible for the close fitting 1:2:1 ratio observed; but the variability within the homozygous classes, not readily separable into groups for the study of ratios, indicated the possible presence of another factor or factors of minor importance. The transgressive segregation obtained suggests that a parent carried some complementary factor without which the awns did not develop.

While most of the later studies on awn inheritance have shown two or more major factors to be involved, the earlier one-factor results receive some support from the study of Marquis X Kota and reciprocal crosses by Clark and Quissenberry (15). A single factor difference explained the results in this cross, a finding in agreement with the earlier results of Hayes and Aamodt for the same cross.

Another single factor difference for awns is reported by Stewart and Price (71) in a cross between Odessa, a short-awned wheat (8 to 24 mm.), and Sevier. An excellent fit was obtained for a 1:2:1 ratio,but it was noted that the awns of the homozygous hybrids in the two parental awn classes tended to be considerably longer on the average than the awns of the parents.

Stewart and Heywood (70) have recently reported on awning in a cross between Federation and a Sevier X Dicklow hybrid known as III C-18. This is another cross between a tip-awned (5 mm.) wheat and a fully awned (73 mm.) form. Four awn classes were used in classification. They

obtained an almost perfect fit in the 9 genotypes postulated on the basis of a two-factor difference. No linkage between these factors could be found such as had been reported by Stewart (68) in the Federation cross on G-149, another Sevier X Dicklow hybrid. This suggests a different genetic constitution for awns in G-149 and III C-18, both of which are fully awned. The factors for awns and spike-density showed no indication of strong linkage in this cross such as had been reported in Kanred X Sevier (69) and Federation X Sevier (67). The homozygous awn 4 group was the only one to show correlation between spike density and awn length.

In a species cross, between _T_. _vulgare_ (Marquis) and _T_. _sphaerococcum_, Miczynski (47) obtained a ratio of 3 awnless and tipped : 1 awned. The _sphaerococcum_ parent was short-awned only, as were the fully awned _sphaerococcum_ segregates, but the awned _vulgare_ segregates showed normal _vulgare_ awning. Evidence is presented to show that there is a correlation between length of awn and spike density and almost complete linkage between the awn type factor and the glume shape factor.

Still another single factor difference for awn characters is reported by Goulden, Neatby, and Welsh (26) for a cross between Marquis and H-44-24. The F_1 was intermediate in type but resembled the Marquis parent more closely. In F_2 a ratio of awnless and intermediates to awned of 791:267, showing a deviation of 2.5 from a perfect 3:1 ratio, was obtained.

Aamodt (1) found no correlation between the presence of awns and growth habit in the progeny of a Kanred (awned winter) X Marquis cross. Gaines and Singleton (25) obtained a slight indication that an awn factor was associated with winter habit but concluded that if there was any linkage between awns and winter habit the number of families studied was too small to determine it.

Awns in relation to yield, quality and disease reaction:- The fact that the awn of wheat is a transpiration organ, and is considered to be of importance in connection with the metabolism of carbohydrates in the wheat kernel,directed the efforts of several investigators towards finding what relation exists between that organ and various physiological processes in the plant. The importance of a possible linkage between awn factors and factors governing resistance or susceptibility to disease is of obvious importance to the plant breeder. So also is any association that can be found between beards and yield or quality of grain.

Hayes (34) reviews the work of Schmid and Perlitius in establishing the importance of the awn as a transpiration organ and the work of the later in showing the effect of the awn on kernel development and size. He also quotes Grantham, who found awnless wheats to be more susceptible to scab, and also somewhat lower in yield than the awned varieties studied. Gaines worked with crosses of Marquis X Preston and Marquis X

Bluestem. His conclusions with regard to the awned character in the progeny of these crosses are as follows:

> " The bearded families average somewhat higher than the awnless families for average length of seed, average percentage of plumpness of seed, and average yield per plant. The awn of wheat is therefore an important organ, and the present tendency to breed only awnless wheats should not be adopted in entirety without further experimental studies."

Clark (10) studied the relation of awning to yield in the Kota X Hard Federation crosses grown at St. Paul, Minn., and Mandan, N. Dak. The F_2 was divided into five awn classes as already described, and the mean yield per plant in each class taken. These data showed a direct relation between awn length and yield at both stations, being more consistent from Mandan, where droughty conditions prevailed, than at St. Paul. The difference between the mean yield of the awnless and awned class was about 15 and 11 per cent. In the light of their probable error these were not very significant, indicating odds of only 9:1. In F_3, grown at Mandan, the results showed the same definite relationship between awn length and yield. The difference between the two extreme classes was 18 per cent or 0.51 ± 0.08 gram, a result that is quite significant. Correlation studies on these data gave small positive values in all cases, but only that for the F_3 at Mandan could be considered significant.

The relation of awnedness to yield and protein content of grain was further studied by Clark (11) in Hard Federation X Propo crosses grown at Davis, California. The awned class exceeded the awnless and apically-awnletted

classes both in yield and in crude protein content. In yield the difference was 21.4% and in protein content it was 10.9%. These figures were considered significant.

Clark, et al., (12) conducted similar studies on Bobs X Propo and Hard Federation X Propo crosses at Davis, California. In F_3 it was found that both crosses gave a slight positive correlation between awn length and increased yield. In the F_2 it had been found that as a result of shattering in the strongly awned classes the reverse was true. In regard to quality and awning the two crosses behaved similarly. In F_2 no significant differences were found between any of the classes, but in F_3 there was a higher protein content in the awned than in the awnless strains. It was also noted that extent of lodging increased in the awned strains.

Results opposite to the above were obtained by Clark and Quisenberry (15) on Kota X Marquis crosses grown at Bozeman, Montana. The lower awn class, in this case awnletted, outyielded the awn class, the difference being statistically significant. Part of this difference was due to greater shattering in the awned class but even when these losses were considered the relative position of the classes was the same. The awned group was found to be significantly higher in protein content than the awnletted.

Hayes, Aamodt, and Stevenson (36), present data to show that the bearded lines of the spring and winter wheats tested, on the average excelled in plumpness the awnless spring and winter lines. In the same study they

found that plumpness of grain and yield were strongly correlated, r being +0.5101 ± 0.0706 for spring wheat and +0.6228 ± 0.0795 for winter wheat. This would seem to indicate that under Minnesota conditions the bearded wheats yield better on the average than the awnless.

Several attempts have been made to correlate awn factors with reaction to various diseases. Some of these have already been mentioned incidentally when reviewing the inheritance of awn factors.

Gaines and Singleton (25) attempted to correlate awn factors and resistance to bunt in a Marquis X Turkey cross. No evidence of linkage was found.

Goulden, et al., (26) found no linkage between awn type and stem rust reaction in the Marquis X H-44-24 cross studied.

Neatby and Goulden (48) studied the relation between awning and field rust reaction in another cross of Marquis X H-44-24 and in H-44-24 X Reward. Independent inheritance was found. In the last mentioned cross chaff pubescence was studied in relation to awning and field rust reaction while in the first-mentioned leaf pubescence was studied in relation to the same two characters. In no case was there any indication of linkage.

Harrington (30) found no correlation between rust reaction and awning in the Marquis X Vernal crosses studied.

Materials and Methods.

The two crosses described in foregoing sections were studied in F_2 and F_3 for segregation of awn characters.

The five awn classes of Clark (10), already described in the literature review, were used as a basis of classification in this study. A scale showing the range for each class and a description of the same were kept at hand while the separation into classes was being made.

In F_2 an attempt was made to place each plant in one of the five classes, and in addition when the plant did not appear to fit the centre of the class range, an estimate was recorded by the use of plus and minus signs to indicate whether the plant approached the upper or lower limit of the class. Also on average measurement, taken in millimeters, was recorded for the awn and beak. These measurements were taken near the centre of the awn or awnlet range and consisted of four readings on two to four well-developed heads.

The F_3 lines were classified plant by plant, no attempt being made to make any finer classification than that provided by Clark's five awn classes. At this stage the three replicates were checked against each other to eliminate any errors that might have crept in during handling and preparing the seed and in seeding. A better judgment on the homozygosity or heterozygosity of the individual lines was also obtained and data for material damaged while in the stook readily corrected. Except in cases where such damage occurred awn classification was made on the material grown in the Campus field.

Experimental Results.

The F_2 segregation for awns in the Kota X Red Bobs crosses agrees very closely with the findings of Clark (10) in some Kota X Hard Federation crosses. His grouping of the awnless classes 1, 2, and 3, and the awned classes 4 and 5, gave a 3:1 ratio with odds of 1.46:1, indicating a close fit. A similar grouping of the segregating F_2 Kota X Red Bobs hybrids is shown in Table XI. The F_2 classification has been corrected by the breeding behavior of F_3 in these data. The odds of 2.46:1 against the occurrence, due entirely to chance, of a deviation as great or greater than the one observed, indicates a good fit to the theoretical ratio.

Table XI - Segregation for awning in Kota X Red Bobs crosses in F_2, and calculation of goodness of fit to a 3:1 ratio.

Awn Class	Numbers			Dev.	P.E.	D/P.E.	Odds.
	Observed		Calculated				
1	49						
2	108	297	288	9	5.72	1.57	2.46:1
3	140						
4	14	87	96				
5	73						

Awn class 1 - awnless
" " 2 - apically-awnletted
" " 3 - awnletted
Awn class 4 - short awned
" " 5 - awned

Note - Description of awn classes, as given by Clark (10) is given on page 43.

While the presence of one major factor difference is indicated by these and Clark's results it is probably concerned principally with the presence or absence of the long, strong Kota awn. The presence of true-breeding lines in classes 2 and 3 requires a two- or multiple-factor hypothesis. Until a detailed analysis is made of the F_3 segregates it can only be said of these crosses that two or more factors must be involved, and that the segregation obtained resembles the results of Clark and others (10,12) in crosses of a similar nature.

Table XII - Segregation for awning in Kota X Garnet crosses in F_2, and calculation of goodness of fit to a 1:2:1 ratio.

Awn Class	Numbers Observed	Numbers Calculated	O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
3	58	85.7	27.7	770.1	9.88
Seg.	173	171.5	1.5	2.3	0.01
5	112	85.7	26.3	689.1	8.04
P = 0.00013				X^2 = 17.93	

In the Garnet X Kota crosses the segregating F_2 population could be grouped, on the basis of F_3 breeding behavior, into three classes. These were awn classes 3 and 5 and a segregating class. Although several F_2 plants had been placed in class 4, all of these were observed to segregate in F_3. Ten plants classified in class 2 in F_2 were included in class 3 as were the few lines segregating for classes 3 and 2. The findings of other workers on similar crosses have shown that a one factor difference explains

most of the results satisfactorily. However, Table XII shows clearly that a single factor difference does not explain segregation for awns following a cross of Garnet and Kota. The deficiency in class 3 and excess in class 5 cannot be explained on the basis of faulty classification, so it must be concluded that probably more than one factor is involved in awn segregation in these crosses.

STRENGTH OF STRAW

Literature Review

The ability of a variety of wheat to resist lodging and stand erect is a very important character economically. The strength of straw that will resist lodging is sought in all hybrid selections made in attempts to improve on the present varieties of wheat grown. However, it is a character that varies so greatly with differences in environment that few genetic studies have been made on it and no factorial explanation of its inheritance attempted.

The Howards (39) made a study of the standing power of wheats which they believed to be due to strong straw and the power to form a strong root system. According to Matsuura (46), they made a cross between a vulgare form with strong straw but inferior rooting capacity and another variety with weak straw but good rooting power. In F_2 all combinations of these characters appeared. This would appear to indicate independent inheritance of the two characters considered by the Howards to produce good standing power.

Harrington (29) made a study of erectness of plant in the parents and hybrids of two durum crosses. Grown in two series of rows the F_4 families of Mindum

X Pentad gave a correlation of $+0.389 \pm 0.037$ and for Kubanka No. 8 x Pentad a correlation of $+0.537 \pm 0.041$. Transgressive segregation occurred in both crosses. He concluded "that in both crosses erectness is dependent on several heritable factors, part of which are present in one parent and part in the other".

Waldron (80) points out that an attempt was made to secure a strong-strawed rust-resistant line from the Kota X Marquis crosses being selected for high yield, quality, and rust resistance. Marquis has a strong straw while Kota is rather weak, but not extremely so. Differences in strength of straw were very apparent in the selections made, the range being from about the strength of Kota to midway between the two parents. No rust-resistant line with strength of straw equal to Marquis was found. However, this author believes the recovery of such a form to be possible. One resistant selection showed considerably weaker straw than the Kota parent.

The association of awnedness and increase in lodging in the Propo hybrids grown at Davis, Calif., noted by Clark, et al. (12), has already been mentioned.

Materials and Methods.

An attempt was made to classify the strength of straw or standing power in each row of the three F_3 series for all four crosses. The parental check rows were first studied and the standing power of the parents taken as the basis of classification. For the purposes in view, up-standing rows of Red Bobs and Garnet were considered as strong and designated S. In each of these varieties some check rows, depending on the location in the field, appeared less upstanding than the strong rows, these being classed as midstrong and designated MS. The midrange of the Kota straw strength was taken as representative of the weak or W class. It showed a considerable tendency toward the production of knee-bent culms that spread outward from the upright plane of the row, and all culms showed a tendency to criss-cross within the row or fall into or against adjacent rows. A stronger class was made between the midstrong class and the weak, into which many of the stronger-appearing Kota parent lines fell, and a weaker class was set up to include those lines that showed distinct signs of lodging. These were known as midweak and very weak and designated respectively MW and VW.

Determinations were made following a period of wind and rain when the earlier lines were in the dough stage but still green, and the later lines contained large watery

kernels. About one week later these determinations were checked. No attempt was made to distinguish heterozygosity, the whole row being taken into consideration. A final rating was made, where the rating in the replicates was at variance, by (i) taking the midclass if three contiguous ratings had been made, (ii) by taking the majority rating where two were in agreement, and (iii) by making adjustments in favor of the class represented by the largest number of plants where the lines were badly reduced in number by the epidemic of cutworms and wind damage already referred to.

Experimental Results.

Table XIII-Distribution for strength of straw in parents and hybrids from Kota X Red Bobs and Kota X Garnet crosses in F_3.

Varieties and Hybrids	Classes for straw strength S	MS	MW	W	VW	Totals
Kota	--	3	50	21	3	77
Red Bobs	33	11	--	--	--	44
Garnet	19	15	2	--	--	36
Kota X Red Bobs	15	64	114	148	52	393
Kota X Garnet	34	74	78	120	35	338

S = strong; MS = midstrong; MW = midweak; W = weak; VW = very weak.

Examination of the data reveals a complex condition. A leaning toward greater weakness than that found in Kota is evident in both crosses. If no transgressive segregation was taking place the expected numbers of hybrid lines in the VW class would be of the order of 11 and 8 instead of 52 and 35 respectively.

By postulating that this increase of numbers in the direction of weaker straw was due to hybrid vigor, causing rapid succulent growth, the necessity of a multiple factor explanation would be overcome. This was done and a simple factor hypothesis tested. To do this the S and MS classes were grouped as "Strong" while the MW, W, and VW classes were grouped as "Weak". Odds against the occurrence of deviations as great or greater than the ones obtained being due to chance were 39:1 and 216:1 in the Kota X Red Bobs and Kota X Garnet crosses respectively. This indicates

that the data does not fit the single-factor expectations.

An attempt was then made to fit the data to a two-factor ratio by grouping the W and VW classes. In this case also the expected ratio was not close enough to the obtained results to warrant the conclusion that segregation for this character was on a two-factor basis. Table XIV and Table XV show the calculation of goodness of fit to the 7:4:4:1 ratio.

Table XIV-Strength of straw segregation in Kota X Red Bobs hybrids and calculation of goodness of fit to a two-factor ratio.

Strength Class	Expected ratio	Numbers Observed	Numbers Calculated	O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
VW+W	7	200	171.9	28.1	789.6	4.59
MW	4	114	98.3	15.7	246.5	2.51
MS	4	64	98.3	34.3	1176.5	11.97
S	1	15	24.6	9.6	92.2	3.75
	P = 0.000045				X^2 =	22.82

From a consideration of these attempts to fit the segregation for straw strength to a single-factor and two-factor ratio it would appear that no such explanation could be offered. No attempt was made to test for goodness of fit to a three-factor ratio, since it was believed that the classification was not fine enough nor could be made accurate enough on a character that varies so greatly

as a result of environmental factors. It was concluded that the complex segregation noted in this study of strength of straw can only be explained on a multiple factor basis.

Table XV - Strength of straw segregation in Kota X Garnet hybrids and calculation of goodness of fit to a two-factor ratio.

Strength Class	Expected ratio	Numbers		O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
		Observed	Calculated			
VW W	7	155	149.2	5.8	33.6	0.23
MW	4	78	85.3	7.3	53.3	0.62
MS	4	74	85.3	11.3	127.7	1.50
S	1	34	21.3	12.7	161.3	7.57
	P = 0.0194				X^2 = 9.92	

CORRELATION STUDIES

General: The importance of studies on correlated inheritance in plant breeding has already been stressed in this paper. In connection with studies on the inheritance of disease reaction the use of correlation as a tool to uncover linkage relations is doubly important. A specific test must, as a rule, be made to determine the presence of factors for resistance and susceptibility. That would be less necessary if such factors were linked with some easily distinguishable morphological character. Under certain environmental conditions it is not always possible to obtain an adequate disease reaction test, making the matter of selecting desirable agronomic forms with disease resistance from a hybrid population more a matter of chance than precision. However, linkage relations when found are seldom of a complete nature, i.e., a certain amount of crossing-over occurs. A knowledge of the strength of linkage is therefore important in estimating the chances of obtaining a desirable recombination where linked desirable and undesirable characters enter a cross.

That qualitative characters may be linked with quantitative and other characters has been amply demonstrated. Lindstrom (43) found that the number of rows in the ear of corn (*Zea mays*), a quantitative character, was associated in inheritance with cob, aleurone, and endosperm color as well as with endosperm texture, all of which are simple qualitative characters. Griffee (82), working with barley (*Hordeum* spp.), demonstrated very

striking linkage relationships between morphological characters and reaction to Helminthosporium sativum. Three factors were found to be concerned with the production of resistance of a certain type. One of these factors was found to be linked with the factor for 2-rowed, one with the factor for rough awn, and another with the factor for white glumes. This author reports the linkage of the factor for early heading, a physiological character, with the factor for 6-rowed and the factor for susceptibility to Helminthosporium sativum.

In the studies here reported an investigation was made of the relation between the reaction of Kota bunt and Red Bobs bunt, and between bunt reaction and some plant characters in the F_3 of Kota X Red Bobs and Kota X Red Bobs. Since the data on bunt reaction was taken on a uniform class basis it was possible to use the correlation coefficient (Pearson's "r") to measure the degree of correlation between the reaction of the two bunts. In the case of the plant characters the classes used could not be considered to have any specific numerical relationship. This necessitated the use of the correlation ratio, "η". A comparison of the values of "r" and "η", by means of Blakesman's test for linearity on some distributions, showed that the correlation ratio was the better measure of correlation for those cases. The probable errors were computed by standard formulae. (9,17,37).

Reactions of Kota bunt and Red Bobs bunt.

Kota X Red Bobs hybrids: The correlation between the reactions of Kota X Red Bobs F_3 lines inoculated with bunt from Kota and from Red Bobs was +0.082 ± 0.059 . This non-significant value was expected in view of the susceptibility of both parents to both smuts. Whether the few lines showing high infection percentages in the Kota bunt test and low percentages in the Red Bobs bunt test, and the fewer numbers that show the opposite reaction, are differential hosts and represent the segregation and recombination of resistance and susceptibility factors can only be judged by further tests. The wide "scatter", covering a range of 80 to 90% in all directions, to be noted on the correlation surface in Table XVI, would suggest, however, that not all of the susceptibility found in the F_3 lines of these crosses is due to the same factors.

Table XVI - Correlation between the reactions of Kota bunt and Red Bobs bunt on Kota X Red Bobs F_3 lines.

		Kota bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Red	0	--	--	--	--	--	1	--	--	--	--	--	1
Bobs	5	--	--	--	--	1	1	1	--	2	1	1	7
bunt	15	--	--	--	--	2	2	1	4	3	3	--	15
infection	25	--	--	--	--	1	3	8	4	2	3	2	23
classes.	35	--	--	--	1	3	4	5	6	6	2	1	28
	45	--	--	--	--	--	6	2	8	8	3	--	27
	55	--	--	--	1	1	2	3	2	2	--	--	11
	65	--	--	--	--	--	1	4	1	5	1	--	12
	75	--	--	--	--	--	--	1	--	1	1	--	3
	85	--	--	--	--	--	--	--	--	1	--	--	1
	95	--	--	--	--	--	--	--	--	--	--	--	--
Totals		--	--	--	2	8	20	25	25	30	14	4	128

r/P.E. = 1.4 $\qquad$ $r = +0.082 \pm 0.059$

<u>Kota X Garnet hybrids</u>: In the Kota X Garnet F_3 lines the correlation between the reactions obtained by inoculation with the same two bunts is indicated by a coefficient of $+0.373 \pm 0.042$. Garnet is resistant and consequently there was a differential reaction between the various hybrid lines. The significant positive correlation indicates that the same factors for resistance in Garnet governs the reaction to both bunts.

As in the case of the Kota X Red Bobs lines, further tests would be necessary to prove the differential nature of certain F_3 lines that were very susceptible to Kota bunt and resistant to bunt from Red Bobs. It should be noted that no lines resistant to Kota and highly susceptible to Red Bobs were found, although some lines were resistant to both kinds of bunt.

Table XVII - Correlation between the reactions of Kota bunt and Red Bobs bunt on Kota X Garnet F_3 lines.

		Kota bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Red	0	3	8	8	13	18	14	5	5	--	2	--	76
Bobs	5	--	--	5	11	12	13	9	5	1	1	--	57
bunt	15	--	1	--	3	8	7	5	6	6	1	--	37
infection	25	--	--	3	--	2	3	1	2	2	1	--	14
classes.	35	--	--	--	--	1	--	--	6	1	--	--	8
	45	--	--	--	--	1	2	--	--	--	--	--	3
	55	--	--	--	--	--	--	--	--	--	--	--	--
	65	--	--	--	--	--	--	--	1	--	--	--	1
	75	--	--	--	--	--	--	--	--	--	--	--	--
	Totals	3	9	16	27	42	39	20	25	10	5	--	196

r/P.E. = 9.0 $\quad$ r = +0.373 ± 0.042

Bunt reaction, awning, and strength of straw.

Kota X Red Bobs hybrids inoculated with Kota bunt: The two plant characters, awning and strength of straw were correlated with the reaction of the hybrid plants to bunt from the parental varieties in the F_3 lines of these crosses.

Negative correlation ratios for reaction to Kota bunt and awning and Kota bunt and straw strength were obtained. These were -0.262 ± 0.037 and -0.303 ± 0.036 respectively. This would seem to indicate that the Kota plant character, weak straw, is associated with susceptibility to Kota smut. Some of the genetic factors governing the expression of this character must be linked with a factor for bunt reaction, and therefore located on the same chromosome. Factors for the Kota plant character, awnedness, would seem to be linked with factors for resistance to Kota bunt.

Kota X Red Bobs hybrids inoculated with Red Bobs bunt: The correlation between the same two characters and reaction to Red Bobs bunt in the F_3 lines of these crosses was positive. The correlation ratio for reaction to Red Bobs bunt and awning was $+0.238 \pm 0.052$, and for reaction to Red Bobs bunt and strength of straw, $+0.204 \pm 0.051$. This would seem to indicate that the Red Bobs character of stronger straw was associated with susceptibility to Red Bobs smut. Some of the genetic factors governing the reaction to this character must be linked with the factors for bunt reaction

Table XVIII - Correlation between the reaction to Kota bunt and awning in Kota X Red Bobs F_3 lines.

		Kota bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Awn	1	--	--	--	1	4	2	10	5	6	8	1	37
Classes	2	--	--	--	1	3	15	11	24	20	8	3	85
	3	--	--	--	2	9	12	23	24	22	1	--	53
	4	--	--	--	--	--	2	3	1	--	--	--	6
	5	--	--	--	2	2	8	6	14	15	5	3	55
Totals		--	--	--	6	19	37	54	67	64	29	12	288

η/P.E. = 7.1 η = -0.262 ± 0.037

Table XIX - Correlation between the reaction to Kota bunt and strength of straw in Kota X Red Bobs F_3 lines.

		Kota bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Strength	W	--	--	--	2	3	3	7	5	8	8	3	39
of	W	--	--	--	1	7	14	21	28	24	10	4	109
straw	MW	--	--	--	1	6	10	14	20	22	6	1	80
classes.	MS	--	--	--	2	3	6	11	11	10	2	3	48
	S	--	--	--	--	--	4	1	3	2	1	--	11
Totals		--	--	--	6	19	37	54	67	66	27	11	287

η/P.E. = 8.4 η = -0.303 ± 0.036

Table XX - Correlation between the reaction to Red Bobs bunt and awning in Kota X Red Bobs F_3 lines.

		Red Bobs bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals.
Awn	1	1	2	2	4	3	4	1	2	1	--	--	20
classes	2	1	4	5	3	12	12	6	2	2	--	--	47
	3	--	3	6	14	7	10	4	5	3	1	--	53
	4	--	--	--	--	--	2	3	1	--	--	--	6
	5	--	--	3	2	8	5	2	5	1	--	--	26
Totals		2	9	16	23	30	33	16	15	7	1	--	152

$\eta/P.E. = 4.6$ $\qquad \eta = +0.238 \pm 0.052$

Table XXI - Correlation between the reaction to Red Bobs bunt and strength of straw in Kota X Red Bobs F_3 lines.

		Red Bobs bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Strength	VW	--	1	3	5	5	4	3	4	--	1	--	26
of	W	2	4	2	9	11	12	8	4	3	--	--	55
straw	MW	--	3	6	2	9	8	2	8	1	1	--	40
classes.	MS	--	1	3	7	8	7	1	--	2	--	--	29
	S	--	--	2	1	1	1	3	--	--	--	--	8
Totals		2	9	16	24	34	32	17	16	6	2	--	158

$\eta/P.E. = 4.0$ $\qquad \eta = +0.204 \pm 0.051$

and therefore located on the same chromosomes. In the case of the awnless character of Red Bobs the significant positive correlation indicates a linkage between awnless factors and resistance to the Red Bobs bunt.

Kota X Garnet hybrids inoculated with Kota bunt: Correlation between the two plant characters, awning and strength of straw, and reaction to Kota bunt was studied in the F_3 lines of the Kota X Garnet crosses. The negative correlation value of -0.203 ± 0.041 obtained for reaction to Kota bunt and strength of straw indicates that the linkage between factors for susceptibility to Kota bunt and for weak straw, noted in the Kota X Red Bobs crosses, has also been carried into this cross.

The negative correlation ratio of -0.235 ± 0.027 obtained for reaction to Kota bunt and awning also parallels the findings in regard to these characters in the Kota X Red Bobs crosses.

Kota X Garnet hybrids inoculated with Red Bobs bunt: Reaction of Red Bobs bunt correlated with strength of straw in these crosses gives a significant positive correlation ratio of $+0.191 \pm 0.043$, indicating that as strength of straw increases the susceptibility to Red Bobs bunt also increases. This parallels the results for the Kota X Red Bobs crosses and would indicate that the same factors for strength of straw probably are present in both Garnet and Red Bobs.

The reaction to Red Bobs bunt and awning show a negative correlation ratio of -0.274 ± 0.041. That the relationship would be of a negative nature is to be expected if some resistance factors of Garnet are linked with awn factors.

Table XXII - Correlation between the reaction to Kota bunt and awning in Kota X Garnet F_3 lines.

		Kota bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Awn	3	1	1	4	6	6	13	5	2	5	1	1	45
Classes	Seg.	2	7	7	13	33	26	15	17	3	2	1	126
	5	--	5	6	18	16	9	7	11	5	3	--	80
Totals		3	13	17	37	55	48	27	30	13	6	2	251

η/P.E. = 8.6 $\eta = -0.235 \pm 0.027$

Table XXIII - Correlation between the reaction to Kota bunt and strength of straw in Kota X Garnet F_3 lines.

		Kota bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Strength	VW	--	4	2	3	--	6	3	6	--	--	--	24
of	W	1	2	7	10	24	19	14	5	4	2	--	88
straw	MW	1	1	3	4	15	14	2	8	3	3	--	54
classes.	MS	1	5	3	12	11	7	3	8	4	1	1	56
	S	--	--	3	4	5	5	3	2	2	--	1	25
Totals		3	12	18	33	55	51	25	29	13	6	2	247

η/P.E. = 4.9 $\eta = -0.203 \pm 0.041$

Table XXIV - Correlation between the reaction to Red Bobs bunt and awning in Kota X Garnet F_3 lines.

		Red Bobs bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Awn	3	16	9	5	2	2	2	--	1	--	--	--	37
classes.	Seg.	44	31	23	9	7	4	1	--	--	--	--	119
	5	28	27	15	4	3	--	1	--	--	--	--	78
	Totals	88	67	43	15	12	6	2	1	--	--	--	234

η/P.E. = 6.7 $\eta = -0.274 \pm 0.041$

Table XXV - Correlation between the reaction to Red Bobs bunt and strength of straw in Kota X Garnet F_3 lines.

		Red Bobs bunt infection classes.											
		0	5	15	25	35	45	55	65	75	85	95	Totals
Strength	VW	10	11	2	1	3	1	--	--	--	--	--	28
of	W	30	30	15	5	2	1	--	--	--	--	--	83
straw	MW	19	11	14	2	3	3	1	--	--	--	--	53
classes.	MS	18	14	6	8	4	1	1	1	--	--	--	53
	S	9	2	6	--	--	--	--	--	--	--	--	17

η/P.E. = 4.5 $\eta = +0.191 \pm 0.043$

Table XXVI - Summary of correlation ratios and correlation coefficients obtained in studies of correlated inheritance in F_3 hybrids of Kota X Red Bobs and Kota X Garnet crosses.

Characters and reactions correlated	F_3 Hybrids	Correlation Coefficient
Kota bunt and Red Bobs bunt	Garnet X Kota	+0.373±0.042
Kota bunt and Red Bobs bunt	Red Bobs X Kota	+0.082±0.059
		Correlation Ratios
Kota bunt and Strength of Straw	Red Bobs X Kota	-0.303±0.036
Kota bunt and Awning	Red Bobs X Kota	-0.262±0.037
Red Bobs bunt and Strength of straw	Red Bobs X Kota	+0.204± 0.051
Red Bobs bunt and Awning	Red Bobs X Kota	+0.238± 0.052
Kota bunt and Strength of Straw	Garnet X Kota	-0.203±0.041
Kota bunt and Awning	Garnet X Kota	-0.235±0.027
Red Bobs bunt and Strength of Straw	Garnet X Kota	+0.191±0.043
Red Bobs bunt and Awning	Garnet X Kota	-0.274±0.041

Summary of correlation values: In Table XXVI a summation is given of the correlation values derived in the course of the inheritance studies just reported. With the exception of one value, they may be considered significant in the light of their respective probable errors. They are, with the exception of the non-significant value, of the same relative order of size and while not large, may be considered highly significant for the purposes of the present study. Attention is drawn to the use by Harris (33) of small but statistically significant correlation coefficients in the study of biological reactions.

SUMMARY

The studies herein reported were made on the F_2 and F_3 progeny of two crosses each of Kota X Red Bobs and Kota X Garnet. The pairs of crosses proved to be identical in nature as shown by similarity in reaction to bunt and loose smut, by seed color segregation, and other characters studied. Consequently data from each pair were merged in the interests of statistical analysis and findings reported as for one cross.

Studies were made of inheritance of (i) resistance to bunt from Kota and bunt from Red Bobs, of (ii) resistance to Kota loose smut, of (iii) the plant characters, seed color, awns, and straw strength, and (iv) correlated inheritance studies made of the reaction of the hybrids of the two crosses to the two bunt forms, and (v) of the reaction of Kota bunt and Red Bobs bunt to awning and strength of straw.

Kota and Red Bobs were each highly susceptible to both Kota bunt and Red Bobs bunt. Garnet was resistant to both bunts but less resistant to the Kota bunt.

The bunt from Kota and the bunt from Red Bobs were considered to be essentially different forms or groups of forms. The Kota bunt was much more virulent than the Red Bobs bunt.

The heritable nature of bunt reaction was clearly demonstrated. The percentage of infection found in the parent lines was recoverdd in the F_3 hybrids but no transgressive

segregation was noted. An indication of the dominance of the bunt-resistance factors was obtained and the presence of several factors governing bunt reaction indicated.

Kota was relatively susceptible to loose smut, Garnet resistant, and Red Bobs immune, under the conditions of test. The heritable nature of the reaction to loose smut was shown by the close check in percentage of infection in the duplicate crosses and the relative percentages of infected lines from the susceptible x resistant (40 %) and susceptible x immune (20 %) crosses.

Two factors are believed to be concerned with segregation for color in the Kota X Red Bobs hybrids. Failure to obtain a good fit for the segregating classes in F_3 was not entirely explainable.

The segregation observed for awn characters in the F_3 lines agreed with the results of Clark (10,12,13) with similar crosses. His method of awn classification (10) was used in preference to that of Stewart, It was concluded that more than one factor was probably involved in awn segregation in the Kota X Garnet hybrids and at least two to several in the Kota X Red Bobs hybrids.

The complex segregation noted in the study of straw strength can only be explained on a multiple factor basis. Transgressive segregation was noted.

In the study of correlation between the reactions of Kota bunt and Red Bobs bunt on Kota X Red Bobs F_3 lines indications were obtained that not all of the susceptibility found was due to the same factors.

The study of correlation between the reactions of Kota X Garnet hybrids to bunt from Red Bobs and Kota indicated that the same factors for resistance in Garnet governs the reaction to both bunts.

Considering the reaction of the two bunts used to inoculate the Kota X Red Bobs hybrids it is to be noted that in both cases we find susceptibility to the smut from the parent associated with the strength of straw found in that parent. Also in both cases the degree of resistance displayed against the smut from the parent is associated with the characteristic awning of that parent. The conclusions to be drawn, from the reaction of the two bunts when used to inoculate the Kota X Garnet hybrids bear out the findings in regard to the Kota X Red Bobs hybrids. Linkage between factors for strength of straw and susceptibility to bunt, and a similar linkage between awning factors and bunt resistance factors are evident.

Taken together the last mentioned findings demonstrate the presence of two linkage groups in wheat concerned with resistance and susceptibility to bunt.

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