INHERITANCE STUDIES
IN A SPRING WHEAT CROSS

Inheritance Studies of Earliness, Bunt Resistance, Awns and Phenol Colour Reactions in a Spring Wheat Cross.

by

Frederick Gfeller

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1. Introduction.

Our greatest wheat growing areas are in Western Canada, hence it necessarily follows that most wheat breeding programmes have as their primary object, the producing of more suitable varieties for that part of the country. A new variety, unless it be early is of doubtful value to Western Agriculture since late maturing sorts are periodically damaged by late summer frosts. The losses due to a reduction of grain yield and grade of wheat as a result of untimely frosts may often total millions of dollars. The inheritance studies of the earliness character in different wheat varieties become of great importance in view of those facts. The number of factors responsible for the expression of 'earliness' in wheat may vary with different varieties, but most investigators report a complex factorial inheritance.

The occurrences of smutted grain in all wheat growing countries is continuously causing serious losses to the farmer. Although, there are plenty of seed disinfectants that will prevent smut infection in wheat, at the same time the root of the evil can only be combatted by appropriately transferring the resistance of one variety on to another differing in this respect.

For some time the various plant breeders have been discussing, whether or not awns of wheat have any bearing upon wheat yield. On the other hand, it seems that a bearded variety of wheat is objectionable from the view point of the farmer, mainly because of less pleasant handling at harvest and threshing time, in comparison with beardless wheats. In both cases, however, the fact remains that extended knowledge of the genetical composition of 'awning' in the existing varieties of wheat may assist in choosing the proper parents for future breeding work.

The phenol colour reaction of wheat varieties has thus far, at least to the knowledge of the author, never been genetically ascertained.

The importance of studying additional inherited characters on wheat by means of a chemical test, and in view of the possibility that varieties might be produced which would be more readily identified in commerce, would be regarded as a great asset to the practical plant breeder and those engaged in research, as well as the grain trade.

2. Description of Parent Material

1. Triticum vulgare lutescens Al.

Var. Garnet Ottawa 652 [x](n = 21)

Description: Plant spring habit, early, short to mid-tall; stem white, slender, weak to mid-strong; spike awnletted, awnlets several, 3 to 15 m.m. long, fusiform, mid-dense to lax, inclined, easily shattered; glumes glabrous, white, long, narrow, shoulders wanting to rounded; beaks narrow, acute, 1 m.m. long; kernels red, short to mid-long, hard, elliptical; germ large; crease narrow, mid-wide; cheeks rounded; brush small, mid-long. Garnet is resistant to bunt.

History - Garnet was originated from a cross made between Preston A. X Riga M. at the Central Experimental Farm, Ottawa, in 1905, by Dr. C.E. Saunders and was distributed for commercial production in the Prairie Provinces of Canada in the spring of 1926.

2. Triticum vulgare lutescens Al.

Red Fife Ottawa 17 [x](n = 21)

Description: Plant spring habit, mid-season to late, tall; stem white, mid-strong; spike apical awned,

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[x] Chromosome counts were made by Dr. R.M. Love.

awnlets few, 2 to 15 m.m. long; fusiform mid-dense to lax, erect to inclined; glumes glabrous, white mid-long, mid-wide; shoulders mid-wide, oblique to square; beaks narrow, acute, 0.5 to 1 m.m. long; kernels red, short to mid-long, hard ovate; germ mid-sized, mid-long.

History: Introduced into Canada indirectly from Scotland through David Fife in 1842. The real origin of this wheat is believed to be Russian. The Red Fife wheat is the foundation stock of all the important bread wheats in Canada and of many of those developed in the United States.

3. Inheritance of Earliness of Heading.

A. Review of the Literature.

The importance of early varieties to the Canadian farmer cannot be over estimated. Indeed, the occurrence of summer frosts in many districts of the West has made the use of early maturing varieties almost obligatory, Newman (41)[x]. As regards the mode of inheritance of earliness, the latter states that it can hardly be regarded as a simple mendelian one. He also claims that a new variety is seldom as early as the earlier parent.

Biffen (3) found in crosses of Polish X Ridit wheat, the F_1 to be intermediate and that earliness and lateness were independently inherited.

Caporn (10) states that systematic experiments on the maturation of cereal crops have not commended themselves to mendelian workers because of the influence due to climatic and edaphic factors. From his observations in oat crosses he concluded that early and late ripening were mendelian characters

[x] Numbers in parenthesis refer to the literature cited.

depending on more than one, and possibly three, factors.

Several wheat crosses made by Thompson (53) gave evidence of a complex segregation of the blending inheritance type. The F_1 was as late as the late parent, the F_2 extended at least from the mean of the early parent to that of the late, while in the F_3, lines earlier than the early parent were obtained.

Florell (20), in a Sunset X Marquis wheat cross, found earliness of heading segregating in the F_2 as 3 early : 1 late. The index of earliness was taken at the time the first head of each plant emerged from the sheath.

Stephens (51) made crosses between six varieties of spring wheat for the purpose of studying the inheritance of earliness of heading. The means of the F_1 and F_2 tended towards that of the early parent; in most cases the F_3 lines showed a degree of earliness within the limits of the parental range. The results were explained on the basis of a number of independent multiple factors having a cumulative effect. With respect to the use of heading dates as an index of earliness he comments that it is less affected by the environment and in general gives a good index of maturity.

Neatby (40) concluded from a study of the F_3 lines of barley crosses that winter vs. spring habit of growth was governed by three main factors; these were also concerned with earliness of heading.

In spring wheat crosses Crescini (13) obtained a 3 late : 1 early ratio in one case and transgressive segregation towards the late parent in another.

The data of David (14) indicate a 9 early : 7 late ratio in the F_2 of barley crosses. The heading dates were taken at one-day intervals.

Smooth-awned varieties of barley were intercrossed and studied in respect of earliness of heading by Johnson and Aamodt (36) but their work was only based on the means of F_3 lines, since they thought that an F_2 plant was not a sufficiently reliable index of heading. Transgressive segregation for both earliness and lateness was observed and the authors suggest that the complex segregation could but be explained by a polymeric factor hypothesis.

Jones et al. (37) studied crosses of several varieties of rice, grown at three different places, in respect of the inheritance of earliness and lateness. In certain crosses one factor, two factors and multiple factors were found to govern earliness of heading. The presence of complementary and modifying factors was evident in all earliness studies. The segregation at the three stations was essentially similar, indicating that earliness reaction of the F_2 plants to an environment is determined largely by their genetic constitution.

De Villiers (54) obtained a 3 early : 1 late ratio in the F_2 of Boer X Fulghum oat crosses. He states that the time of heading was influenced by both maximum and minimum temperatures.

From the foregoing literature discussion it is apparent that the inheritance of earliness of heading varies with different varieties of the same species, as much as it does with different genera. In most studies there were one to three factors concerned in the inheritance of earliness, and furthermore, the best results were obtained when the data of the F_1 and F_2 as well as those of the F_3 had been observed. The genotype of a plant is of greater influence in respect of the expression of earliness than is the influence of wide ranges in the environment encountered in this experiment.

B. Experimental Procedure and Data

Seeds of single line selections of the early parent Garnet Ott. 652 and the late parent Red Fife Ottawa 17 were sown at different dates in the greenhouse during the fall of 1933. During the following winter many F_1 seeds were produced, and later planted in a bird proof cage in the spring of 1934. In the fall of 1934, the seeds of F_1 plants 52 A, B and C, were planted in the greenhouse pot cultures for earliness of heading studies in the subsequent F_2 generation. Some F_1 seeds as well as parent seeds were also sown for comparative heading date studies. The dates of heading in both field and greenhouse studies were based on the emergence of the topmost spikelet from the leaf sheath. The record of those dates was attached to each plant by means of a string tag.

Since the plants grown in the greenhouse in 1934-35 were influenced by sterility due to artificial environment, the seed-set of these F_2 plants was very much reduced. Consequently in many cases the F_3 lines consisted of only a few plants.

In the field in 1935 seeds of F_1, F_2 and F_3 generations were planted on the same day spaced three inches apart in the rows and with seven inches between rows. All the greenhouse and field data are presented in the following tables.

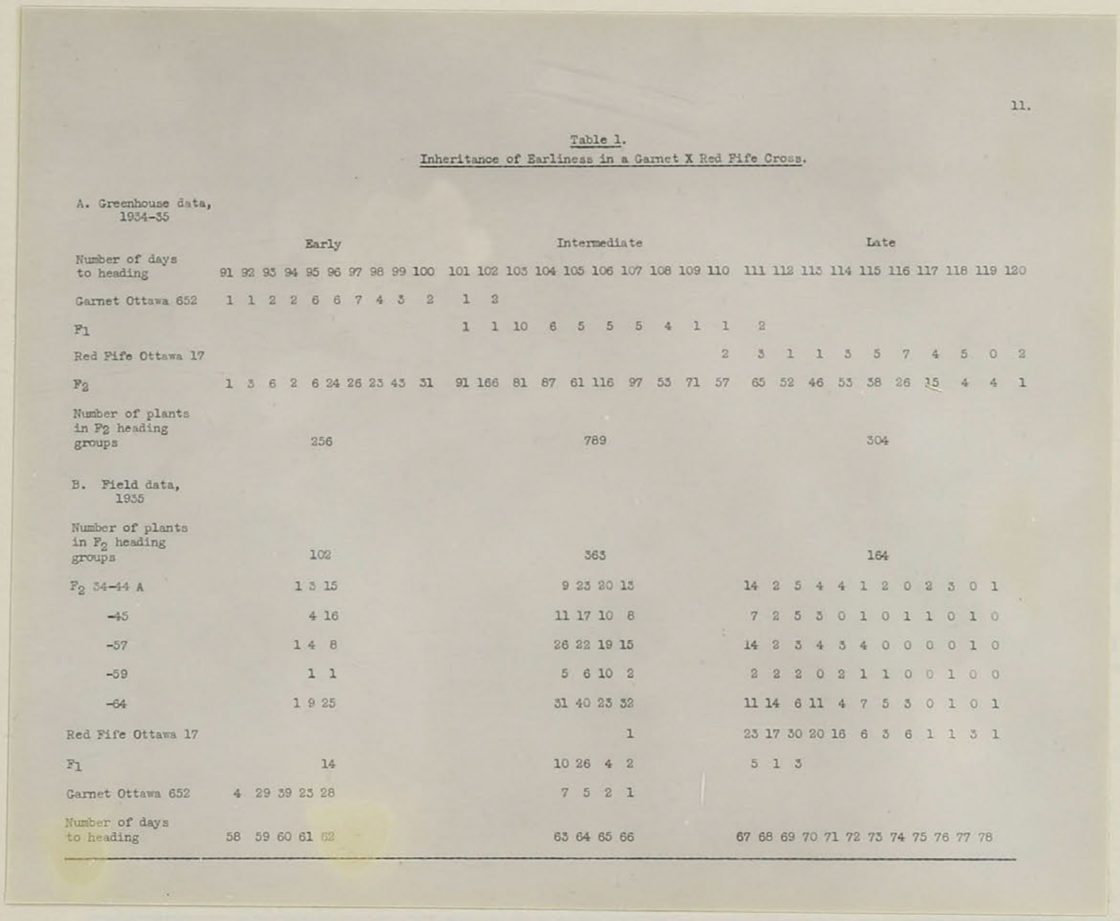

Table 1.
Inheritance of Earliness in a Garnet X Red Fife Cross.

A. Greenhouse data, 1934-35

	Early										Intermediate										Late									
Number of days to heading	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Garnet Ottawa 652	1	1	2	2	6	6	7	4	3	2	1	2																		
F_1											1	1	10	6	5	5	5	4	1	1	2									
Red Fife Ottawa 17																				2	3	1	1	3	5	7	4	5	0	2
F_2	1	3	6	2	6	24	26	23	43	31	91	166	81	87	61	116	97	53	71	57	65	52	46	53	38	26	15	4	4	1
Number of plants in F_2 heading groups	256										789										304									

B. Field data, 1935

Number of plants in F_2 heading groups	102					363				164											
F_2 34-44 A			1	3	15	9	23	20	13	14	2	5	4	4	1	2	0	2	3	0	1
-45				4	16	11	17	10	8	7	2	5	3	0	1	0	1	1	0	1	0
-57			1	4	8	26	22	19	15	14	2	3	4	3	4	0	0	0	0	1	0
-59				1	1	5	6	10	2	2	2	2	0	2	1	1	0	0	1	0	0
-64			1	9	25	31	40	23	32	11	14	6	11	4	7	5	3	0	1	0	1
Red Fife Ottawa 17									1	23	17	30	20	16	6	3	6	1	1	3	1
F_1					14	10	26	4	2	5	1	3									
Garnet Ottawa 652	4	29	39	23	28	7	5	2	1												
Number of days to heading	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78

From the foregoing table it may be seen that the segregation for earliness and lateness were of a similar type in the greenhouse and in the field. It was also worth while noting that in the greenhouse each of the heading classes embraced a ten-day class interval, while in the field the early class takes in five days, the intermediate four days and the late one twelve days. The grouping of heading dates in the F_2 was in both cases based on the parents and F_1 behaviour.

Table 2.

Goodness of fit of the F_2 population, grown in the greenhouse, tested against a 9 intermediate : 3 early : 4 late ratio.

	Observed	Calculated	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
Intermediate	789	758.8 (9)	30.2	912.04	1.2019
Early	256	252.9 (3)	3.1	9.61	.0379
Late	304	337.3 (4)	33.1	1095.61	3.2481
Total	1349	1349.0		X^2 =	4.4879
				P =	.1 to .2.

By looking up Fisher's (17) probability table on the distribution of X^2 for n - 1 degrees of freedom, it was found that P = .1 to .2. This is a fairly significant value and indicates that the assumption of two factors giving 9 intermediate : 3 early ; 4 late hypothesis fits the data satisfactorily, since a deviation as great or greater would be expected to occur in 10 to 20 percent. of the cases. Fisher gives the lowest limit of significance as P = .05. (In any future application of the value of P, no explanation will be presented as to its interpretation.)

Table 3.

Goodness of fit of the F_2 population, grown in the field, tested against a 9 intermediate : 3 early : 4 late ratio.

	Observed	Calculated	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
Intermediate	363	353.8 (9)	9.2	84.64	.2392
Early	102	119.0 (3)	17.0	289.00	2.4285
Late	164	157.2 (4)	6.8	46.24	.2941
Total	629	629.0		X^2 =	2.9618

This is a very good fit, for P = .2 to .3.

The X^2 test of both greenhouse and field grown F_2 plants gave uniformly a value of P well within the limit of significance, giving evidence of the fact, that although, the plants were grown in two entirely different environments the segregation ratio remained unchanged (37).

Since it was impossible to sharply divide all segregating F_3 lines according to their genotypic expectations, due to the occurrence of overlapping in the earliest and also intermediate F_3's, the author will present only the general trend of those lines bearing out the F_2 factorial hypothesis.

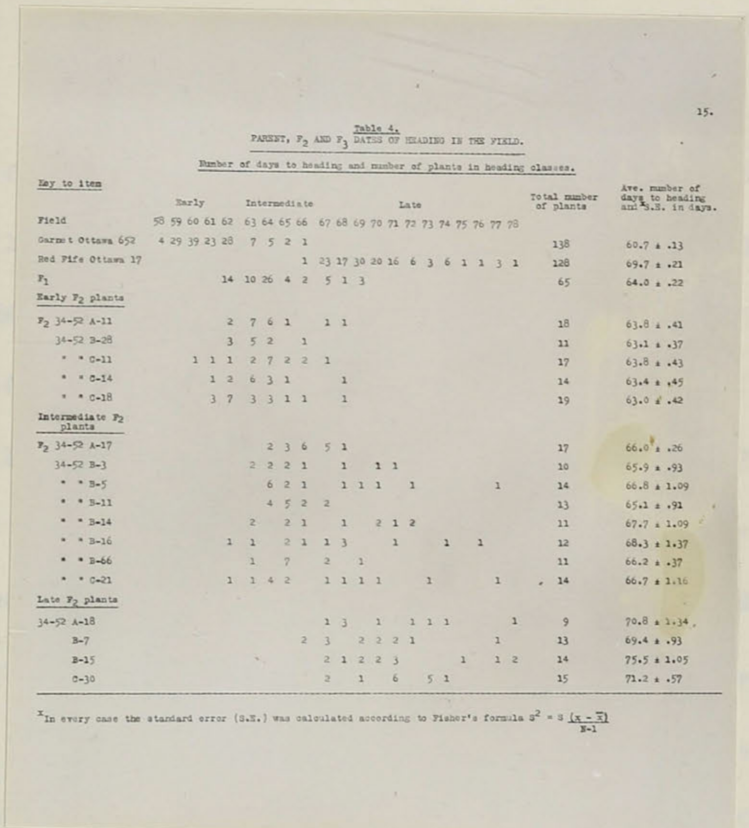

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Table 4.
PARENT, F_2 AND F_3 DATES OF HEADING IN THE FIELD.

Number of days to heading and number of plants in heading classes.

Key to item	Early					Intermediate				Late												Total number of plants	Ave. number of days to heading and ˣS.E. in days.
Field	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78		
Garnet Ottawa 652	4	29	39	23	28	7	5	2	1													138	60.7 ± .13
Red Fife Ottawa 17									1	23	17	30	20	16	6	3	6	1	1	3	1	128	69.7 ± .21
F_1					14	10	26	4	2	5	1	3										65	64.0 ± .22
Early F_2 plants																							
F_2 34-52 A-11					2	7	6	1		1	1											18	63.8 ± .41
34-52 B-28					3	5	2		1													11	63.1 ± .37
" " C-11			1	1	1	2	7	2	2	1												17	63.8 ± .43
" " C-14				1	2	6	3	1			1											14	63.4 ± .45
" " C-18				3	7	3	3	1	1		1											19	63.0 ± .42
Intermediate F_2 plants																							
F_2 34-52 A-17							2	3	6	5	1											17	66.0 ± .26
34-52 B-3						2	2	2	1		1		1	1								10	65.9 ± .93
" " B-5							6	2	1		1	1	1		1					1		14	66.8 ± 1.09
" " B-11							4	5	2	2												13	65.1 ± .91
" " B-14						2		2	1		1		2	1	2							11	67.7 ± 1.09
" " B-16					1	1		2	1	1	3			1			1		1			12	68.3 ± 1.37
" " B-66						1		7		2		1										11	66.2 ± .37
" " C-21					1	1	4	2		1	1	1	1			1				1		14	66.7 ± 1.16
Late F_2 plants																							
34-52 A-18										1	3		1		1	1	1				1	9	70.8 ± 1.34
B-7									2	3		2	2	2	1					1		13	69.4 ± .93
B-15										2	1	2	2	3				1		1	2	14	75.5 ± 1.05
C-30										2		1		6		5	1					15	71.2 ± .57

ˣIn every case the standard error (S.E.) was calculated according to Fisher's formula $S^2 = S\,\frac{(x - \bar{x})}{N-1}$

In the preceding table it was illustrated that early plants may be selected in the F_2 generation, for most of them will remain so in the F_3 lines. The same method of selection holds true for the intermediate and late phenotypes. It was also observed that in all cases there occurred a shift towards lateness. The early hybrids are later than the early Garnet parent, while the intermediates were later than the F_1, and the late segregates later than the parent Red Fife. This occurrence must have been due to the unsuitability of the Red Fife variety in this season, since its spread of heading was at least as wide in the field as it was in the greenhouse, while the heading periods of Garnet and the F_1 narrowed their limits. The presence of modifying factors inhibiting the occurrence of the earliness of Garnet wheat seems evident.

The genotypes of the parents F_1, and F_2, on the basis of the data presented in tables 1, 2, 3 and 4 may be regarded as follows:

Early parent Garnet AAbb x Late parent Red Fife aaBB
F_1 intermediate AaBb
F_2 Garnet range intermediate F_1 range Red Fife Range
3 Ab : 9 AB : 3 aB : 1 ab

	F_2 genotypes		F_3 breeding behaviour
9	1	AABB	True breeding intermediate
	2	Aa BB	3 interm. : 1 late
	2	AABb	3 " : 1 early
	4	AaBb	9 " : 3 early : 4 late
3	1	AAbb	True breeding early
	2	Aabb	3 early : 1 late
4	1	aaBB	True breeding late
	2	aaBb	All late
	1	aabb	True breeding late

All late F_2 plants are expected to produce all late F_3 lines. That this was the case, may be seen in table 4.

In the next table a number of F_3 lines composed of 20 plants in each awn class and heading date groupings are presented.

Table 5.

Number of days to heading in the F_3 awn classes.

Population Nos.	Awn class	Ave. no. of days to heading in the field and S. E in days	Classification of F_2 plants in greenhouse.
34-52 B1-4	Bald	65.7 ± .81	Early
34-52 B12-14	"	67.4 ± .60	Intermediate
34-52 B17-20	"	68.8 ± .81	Late
34-52 B21-22	Ap.awns	65.7 ± .61	Early
34-52 B37-39	"	67.6 ± .91	Intermediate
34-52 B43-45	"	70.4 ± .97	Late
34-52 B46-49	Awnlet	64.2 ± .78	Early
34-52 B61-63	"	66.8 ± .72	Intermediate
34-52 B67-68	"	68.0 ± .51	Late
34-52 B18	Awned	62.0 ± .32	Early
34-52 B72-74	"	67.6 ± .66	Intermediate
34-52 B75	"	67.7 .73	Late

The evidence presented in the above table shows that earliness of heading in wheat may be obtained in all awn classes (3, 25).

C. Summary

1. The F_1 of a cross between the early parent Garnet and the late parent Red Fife, was found to be intermediate in respect to earliness.
2. The F_2 segregated in a 9 intermediate ; 3 early : 4 late ratio in the greenhouse as well as in the field.
3. Along with the presence of 2 complementary factors, evidence of the action of some modifying factors was also obtained, especially in the early and intermediate F_3 lines.
4. The genotype of a plant was of much greater influence in respect of the expression of earliness than was the influence of wide ranges in the environment upon that plant.
5. The heading period of the late parent and hybrids extended over a uniform number of days in both field and greenhouse, while the early parent narrowed its heading period in the field.
6. The classification of the late F_3 lines was facilitated through the fact, that its heading period in the field extended over more days than either the early or intermediate lines.
7. Inheritance of earliness and awns appeared in-

dependent, since early, intermediate and late F_3 lines could be obtained in each awn class.

Inheritance of smut resistance

A. Review of literature.

The literature on the two species of stinking smut or bunt, *viz.* *Tilletia tritici* (Bjerk.) Wint. and *T. laevis* Kühn, is very voluminous from the viewpoints of the agricultural economist, geneticist and plant pathologist. This smut is a more or less troublesome disease wherever wheat is cultivated.

Losses due to bunt have been invariably estimated to amount to millions of dollars annually. Heald (32) states that the financial losses are due to:

1. Increased cost of production due to seed treatment, soil sanitation and cultural practices designed to reduce infection.
2. The reduction in yield per acre.
3. The lowering of grade or quality.
4. The losses from separator and grain fires caused by smut explosions.

Flor *et al.* (19) found that the correlation coefficient between yield and percentage of bunt was -0.81 ± 0.05 for the susceptible variety Hybrid 128 and -0.60 ± 0.69 for the resistant variety Ridit. The latter showed an average percentage of smut of 1.13, which in turn caused a reduction in yield of 11.3 per cent.

In 1930 Heald and Gaines (33) made an analysis of yield tests that had been conducted over a period of years, and found that 25.8 per cent. of smutted heads reduced the yield by 23.0 per cent.

It was estimated by Bressman (5) that in the Pacific Northwest the loss due to bunt is about ten million dollars per annum.

The following citations of literature present the problems of the geneticist and plant pathologist:

Woolman (56) ascertained that the fungus enters both the resistant and susceptible host varieties, but states that the menace to the resistant host is ended before the emergence of the true leaves. Zade (57) also pointed to the fact that the smut organism gained entrance to the immune varieties, and although not reaching the reproductive stage, it nevertheless reduced the yield owing to a reduction in stand. This phenomenon he termed "latent infection". In accordance with the results of his experiments he recommends the use of fungicides for both resistant and susceptible varieties. This statement almost implies that the breeding of smut resistance is economic fallacy, but it is obvious that if all varieties are resistant and no spores are being formed, then the use of fungicides for the prevention of smut will be entirely unnecessary. In this respect Aamodt (1) states that the spread of the smut fungus in Western Canada was due to the introduction of many susceptible varieties of wheat and the presence of many physiologic forms of smut.

In 1924 Faris (16) discovered wheat varietal differences in temperature requirements for infection of the bunt organism. Furthermore, he concluded that varieties should be tested with more than one spore collection in order to obtain a real index of varieties. His work may be regarded as the first evidence of physiologic specialization of the bunt organism.

Rodenhiser and Stakman (46) identified three forms of _T_. _laevis_ and two of _T_. _tritici_ on differential wheat varieties.

Through a varietal test with a bunt collection Gaines (24) found that the following varieties were immune to the fungus: Martin, Hussar and White Odessa. In a bunt resistance breeding programme Briggs (7) found that the Martin and Hussar wheat varieties carried the same single dominant factor pair for resistance. However, later (8) he found in crosses of Hussar and Martin a selection 1418 with an extra factor for resistance. Accordingly he designated the resistance of Martin as MM and that of Hussar as HHMM, the M factors in both varieties being allelomorphic and the H factor being the extra resistance factor found in Hussar Selection 1418.

In 1933 Briggs (9) obtained data indicating the presence of a third factor for resistance to *T. tritici* by crossing Hussar and Turkey wheats. The presence of a recessive factor for resistance in Florence wheat points to the possibility of a fourth factor.

This is an excellent illustration of how constructive plant breeding can isolate genetic factors for resistance to certain physiologic forms of bunt and gradually build up an accumulated resistance. The genotypic composition of a variety as regards bunt resistance can only be ascertained by the use of a comparatively pure physiologic form of the fungus (Bressman (5)).

Dillon Weston (15) has shown that the resistance of the Sherman variety of wheat may be broken down by continuously inoculating the host with its own bunt. He states therefore: "It is apparent from these results that a pathogen may be selected from a population to which the host is susceptible, in the same way as the plant breeder may choose a unit from a population of a host variety for resistance to a given pathogen."

Hanna (29) and Bressman (5) have proven that the optimum temperature requirements for spore germination of different physiologic forms of smut vary considerably. The latter claimed that certain forms germinate at 6° C. and not at all at 18°C.

In the light of the above remarks it seems apparent that every environmental coincidence may have a prevalent form of smut as well as variety of wheat; and therefore it should not be exceedingly difficult to produce the desirable varietal resistance towards a particular pathogen unless there exists a high correlation between the host and parasite requirements. Smith (49) inoculated Jenkins and Hope wheats with the same physiologic form of _T. tritici_ and grew them continuously at low temperatures, as well as at alternatively high and low temperatures. The experiment revealed that Hope was resistant at high temperatures and susceptible at low ones, while Jenkins was susceptible in both cases.

Again, there exists the possibility that the smut pathogen readily hybridizes or mutates to adapt itself to the host (11, 18). It stands to reason that a proven pure physiologic form will produce nothing new unless a mutation of some kind occurs. The results obtained by the present investigator tend to show that resistant varieties may be bred successfully, and that the pure line method of obtaining bunt is of great value in ascertaining the genetic constitution of the same.

In connection with the above dissertation it is of great value to know that Smith (48) ascertained that the two species of smut rarely occur on the same wheat spike. The present author has also noticed that under ordinary bunt-favourable conditions only the best adapted form of bunt infects the host (see below).

From the literature reviewed it appears that the geneticist and plant pathologist are gradually solving the smut problem and are undoubtedly helping to balance the budget of the farmer.

B. Experimental procedure and data.

In the spring of 1934 chlamydospore collections of T. tritici and T. laevis were used in inoculating the seeds of the parent varieties Garnet Ottawa 652 and Red Fife Ottawa 17. The bunt inocula were used for some time in breeding work in the Cereal Division, Ottawa, previous to this investigation, and may be regarded as fairly pure. The bunt from the infected plants was used in the greenhouse in the winter of 1934-35 for inoculation of the parents, F_1 and F_2 seeds.

Before using the inocula a bunt ball from each head was examined under a microscope for identification purposes. Smut balls of each species were then separately crushed in a petri dish, the pericarps of the grains were then removed by means of a pair of tweezers, and the seed was placed in the dish, well shaken, and each kernel removed with the forceps.
The Tilletia species secured from both parents were kept separate throughout the studies, except in one trial, where the four collections were mixed proportionately by taking the same number of bunt balls from each head to make a mixed inoculum. During the first four weeks of the growing season in the greenhouse pot cultures, the plants were kept at a temperature of about 50° F., a temperature desirable for germination (28),

and a moisture content of approximately 20 per cent. This appears to be a good combination of moisture and temperature for obtaining a high infection percentage. The following tables give an account of the numbers of bunted and resistant plants, as well as the percentages of resistance in a Garnet X Red Fife cross.

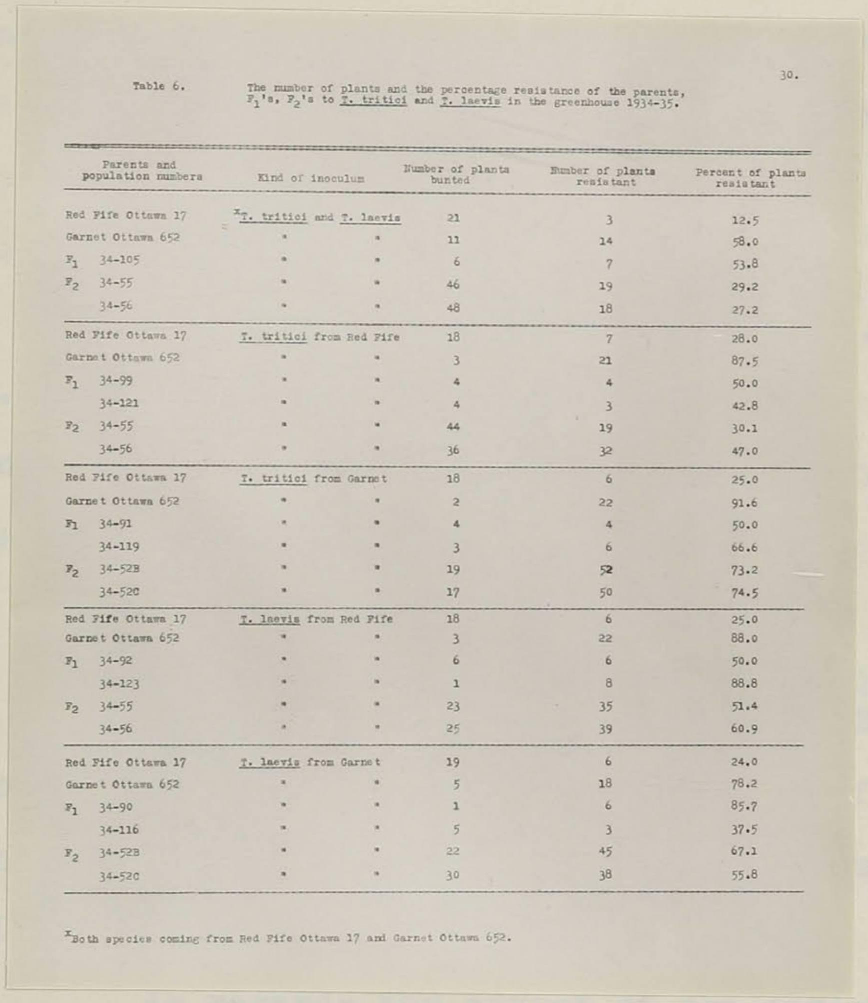

Table 6. The number of plants and the percentage resistance of the parents, F_1's, F_2's to *T. tritici* and *T. laevis* in the greenhouse 1934-35.

Parents and population numbers	Kind of inoculum	Number of plants bunted	Number of plants resistant	Percent of plants resistant
Red Fife Ottawa 17	[x]*T. tritici* and *T. laevis*	21	3	12.5
Garnet Ottawa 652	" "	11	14	58.0
F_1 34-105	" "	6	7	53.8
F_2 34-55	" "	46	19	29.2
34-56	" "	48	18	27.2
Red Fife Ottawa 17	*T. tritici* from Red Fife	18	7	28.0
Garnet Ottawa 652	" "	3	21	87.5
F_1 34-99	" "	4	4	50.0
34-121	" "	4	3	42.8
F_2 34-55	" "	44	19	30.1
34-56	" "	36	32	47.0
Red Fife Ottawa 17	*T. tritici* from Garnet	18	6	25.0
Garnet Ottawa 652	" "	2	22	91.6
F_1 34-91	" "	4	4	50.0
34-119	" "	3	6	66.6
F_2 34-52B	" "	19	52	73.2
34-52C	" "	17	50	74.5
Red Fife Ottawa 17	*T. laevis* from Red Fife	18	6	25.0
Garnet Ottawa 652	" "	3	22	88.0
F_1 34-92	" "	6	6	50.0
34-123	" "	1	8	88.8
F_2 34-55	" "	23	35	51.4
34-56	" "	25	39	60.9
Red Fife Ottawa 17	*T. laevis* from Garnet	19	6	24.0
Garnet Ottawa 652	" "	5	18	78.2
F_1 34-90	" "	1	6	85.7
34-116	" "	5	3	37.5
F_2 34-52B	" "	22	45	67.1
34-52C	" "	30	38	55.8

[x] Both species coming from Red Fife Ottawa 17 and Garnet Ottawa 652.

From the foregoing table it may be seen that Garnet shows considerable resistance to the physiologic forms present (1, 6, 26, 38), at least when compared with the susceptible parent, Red Fife (6). The F_1 hybrid of the cross tends to be uniformly intermediate with respect to smut resistance. In the case where the mixed _Tilletia species_ were used there occurred a significant drop in resistance of both parents and hybrids.

The F_2 families inoculated with _T. tritici_ and _T. laevis_ mixture showed the following percentages of infected heads with the two species (one bunt ball from each head was examined under the microscope)[x]:

	T. tritici	_T. laevis_
Family 34-55	75.0%	25.0%
Family 34-55	76.0%	24.0%

This appears to be a typical indication of the fact that the species of bunt having the optimum condition will infect the host.

As regards the effect of the various individual inocula derivatives on the F_2 population it seems

[x] Determined by Mr. I.L. Conners.

apparent that only slight differences exist in respect of virulence. No attempt is being made to explain the above result on a factorial basis, but Table 7 summarizes the comparative resistance of parents and hybrids:

Table 7.

Summary of results showing comparative resistance of parents and hybrids.

Key to items	Number of plants bunted	Number of plants resistant	Percentage of plants resistant
Red Fife Ottawa 17	104	28	21.2
Garnet Ottawa 652	24	97	80.1
Total for parents	128	125	49.4
F_1	34	47	58.0
F_2	320	347	52.0

The ratio of susceptible to resistant plants approaches nearest to a 1: 1 ratio. Note that families 34-55 and 34-56 are split up into three parts, and families 34-52B and 34-52C into two parts. This will, if necessary, permit correlation work in the F_3 lines. Gaines and Smith (24) divided seed of each F_2 plant from a cross between Hohenheimer and White Odessa into three parts which were inoculated with three physiologic forms of T. tritici. Subsequently, with the aid of correlation, they determined that the same factor in Hohenheimer governed the resistance to two forms.

Experiments in the field in 1935.

The resistant plants of all F_2 families from the greenhouse were subsequently planted in the field. The F_2 and F_3 seeds were inoculated the same way as formerly in the greenhouse, but the inoculum consisted of Tilletia chlamydospores coming from each of the parents after screening through the F_2. The identity of the inoculum was kept throughout the experiment, for example, the bunt used on the F_2 family 34-55 and which came from a specific parent was used only on those respective F_3 plants. The mixed inoculum of Tilletia was composed of equal parts of T. laevis and T. tritici coming from Red Fife and Garnet through the F_2.

The earliest possible date for seeding was April 25th and at that time the temperature of the soil as determined by a soil thermometer was 42.0° F. and for the first three weeks it did not exceed 55° F. The soil was of a sandy clay nature with good moisture holding capacity.

The seeds were sown in head rows three inches apart in the row and the rows spaced seven inches apart. In most cases 24 seeds were sown in each row. Between each of the test groups the parents were sown for comparative resistance. After the plants were fully mature they were pulled and tied into sheaves for laboratory examination, the results of which are as follows:

Table 8.

Number of bunted and resistant plants in the F_2.

Parent and population numbers	Kind of inoculum	Number of bunted plants	Number of resistant plants	Percent. of resistant plants.
Red Fife Ottawa 17	*T. tritici* and *T. laevis*	27	36	57.2
Garnet Ottawa 652	"	7	61	89.9
F_2 34-105-1	"	4	24	85.8
-2	"	6	16	75.0
-3	"	5	13	72.3
-4	"	4	10	71.5
F_2 34-117-1	"	1	12	91.3
	Total F_2	26	92	Average 77.9 ± 3.80

Table 9.

Number of susceptible and resistant plants in F_3 segregating lines

Population numbers	Kind of inoculum	Number of bunted plants	Number of resist. plants	Percent of resist. plants
F3 34-55-1	[x]*T. tritici* and *T. laevis*	3	11	78.5
-3	"	5	17	77.3
-4	"	3	21	87.5
-7	"	6	20	77.0
-8	"	6	14	70.0
-10	"	6	10	62.5
-11	"	5	11	68.8
-12.	"	2	4	66.7
-13	"	7	24	77.5
Total		43	132	Ave. 75.4 ± 2.71
F_3 34-56-1	*T. tritici* and *T. laevis*	7	12	63.2
-6	"	7	21	75.0
-7	"	2	17	89.5
-8	"	3	13	81.3
-11	"	3	14	82.4
-12	"	2	9	81.9
-13	"	2	3	60.0
-14	"	6	14	70.0
Total		32	103	Ave. 76.3 ± 3.84

[x] From the mixed inoculum 60 plants were chosen at random, and one smut ball from each head examined for the presence of *T. laevis* and *T. tritici.* It was found that 2 plants (3.3%) were infected with *T. laevis.* The bunt species having the optimum condition, germinated and infected the plants, was therefore T. tritici.

From the two preceding tables it is evident that the resistance of both F_2 and F_3 hybrids is about 75.8 per cent. On the basis of a single factor difference between the parents one would expect 75.0 per cent. resistant, and 25.0 per cent. susceptible plants. The difference between the percentages of resistance in the F_2 and F_3 generations is significant since it exceeds twice the standard error. Nevertheless, the single determination of the susceptible parent shows a percentage resistance of only 57.2. It is obvious that one may either choose the limits of susceptibility based on the standard error, 70 per cent., or the parent Red Fife. Mention may be made that whichever way one chooses the result will be borne out, accordingly, in the goodness of fit test with the hybrid plants and lines.

Table 10.

Summary of all F_2 and F_3 segregating lines of observed smutted and resistant plants as tested against a 3 : 1 ratio.

	Observed	Calculated	O - C	$(O - C)^2$	$\frac{(O-C)^2}{C}$
Susceptible	101.0	106.7 (1)	5.7	32.49	0.3045
Resistant	326.0	320.3 (3)	5.6	32.49	0.1014
Total	427.0	427.0		X^2 =	0.4059
	This is a very good fit.			P =	.50 to .70.

Table 11.

F_3 lines resistant and susceptible to *T. tritici* and *T. laevis*

Parent and population numbers	Number of plants susceptible	Number of plants resistant	Percent. of plants resistant
Garnet Ottawa 652	7	61	89.9
34-55-5	0	14	100.0
-6	0	14	100.0
-9	1	12	92.4
-15	0	18	100.0
-16	2	16	89.9
34-56-3	0	15	100.0
-4	1	11	91.7
-5	0	14	100.0
-9	0	18	100.0
-10	0	16	100.0
-15	0	12	100
Total F_3	4	160 Average	97.6 ± 1.32
Red Fife Ottawa 17	27	36	57.2
34-55-2	3	3	50.0
-14	6	5	45.5
34-56-2	8	10	55.6
Total F_3	17	18	51.4 ± 3.58

The resistance index in the above table is unusually high, while the susceptibility of the F_3 lines is well within the limit of the S.E.

Table 12.

Observed and calculated agreement of F_3 lines resistant, segregating and susceptible to *T. tritici* and *T. laevis*.

	Observed	Calculated	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
Susceptible	3	7.7 (1)	4.7	22.09	2.8688
Segregating	17	15.6 (2)	1.4	1.96	.0218
Resistant	11	7.7 (1)	3.3	10.89	1.4142
Total	31	31.0		X^2 =	4.3048
	This is a good fit, for			P =	.1 to .2

As previously stated, there was only 3.3% of *T. laevis* admixture, consequently the single resistant factor found should be considered as a gene partially dominant and resisting *T. tritici*.

The next experiment deals with the form of *T. tritici* which had been passed through Red Fife Ottawa 17 and the F_2 hybrid.

Table 13.

F_2 segregation into plants susceptible and resistant to *T. tritici* coming from Red Fife through F_2 hybrid.

Parent and population numbers	Number of plants susceptible	Number of plants resistant	Percent. of plants resistant
Red Fife Ottawa 17	29	38	56.8
Garnet Ottawa 652	7	62	89.9
F_2 34-99	4	11	73.4
34-121-1	3	9	75.8
-2	2	7	77.8
-3	4	18	81.9
Total F_2	13	45	Average 77.5 ± 2.14

Table 14.

Number of susceptible and resistant plants in F_2 segregating lines.

Population numbers	Number of plants susceptible	Number of plants resistant	Percent. of plants resistant
34-55-3	5	12	70.6
-4	2	7	77.8
-5	2	7	77.8
-7	2	16	88.9
-8	2	5	71.5
Total	13	47 Average	78.3 ± 3.65
34-56-3	3	11	78.6
-6	3	11	78.6
-7	1	3	75.0
-11	4	10	71.5
-12	3	10	77.0
-13	3	12	80.0
-14	2	12	85.0
-15	3	10	77.0
-16	4	14	77.8
-17	1	6	85.8
-20	2	6	75.0
-22	5	14	73.7
-24	4	15	78.9
-25	4	17	81.0
-26	2	8	80.0
-28	6	15	71.5
-30	2	6	75.0
Total	52	180 Average	77.5 ± .93

Table 15.

Summary and goodness of fit, of smutted and resistant plants in the F_2 and F_3.

	Observed	Calculated	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
Susceptible	65	73 (1)	8	64.0	.8767
Resistant	227	219 (3)	8	64.0	.2922
Total	292	292			$X^2 = 1.1689$

The 3 resistant : 1 susceptible ratio is very good, because P = .2 to .3.

Table 16.

The resistant and susceptible F_3 lines.

Parent and population numbers	Number of plants susceptible	Number of plants resistant	Percent. of plants resistant
Garnet Ottawa 652	7	62	89.9
34-55-2	0	8	100.0
-9	1	19	95.0
-11	0	17	100.0
-12	0	13	100.0
34-56-1	0	11	100.0
-2	1	10	91.0
-4	1	9	90.0
-5	1	13	92.9
-8	1	14	93.4
-9	2	18	90.0
-27	1	14	93.4
-29	1	14	93.4
Total F_3	33	41	Average 55.4 ± 5.37

Table 17.
Goodness of fit of resistant, segregating and susceptible F_3 lines.

	Observed	Calculated	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
Susceptible	5	9.5 (1)	4.5	20.25	2.1315
Segregating	22	19.0 (2)	3.0	9.00	.4736
Resistant	11	9.5 (1)	1.5	2.25	.2368
Total	38	38.0		χ^2 =	2.8419
Again a very good agreement, for				P =	.2 0.3

From the tables dealing with the inheritance of resistance to the form of *T. tritici* coming from Red Fife and the F_2 hybrids, it is observed that the single factor hypothesis is an adequate explanation of the results. The points of susceptibility and resistance were taken at 70.0 and 80.0 per cent., respectively.

The following table gives an account of the inheritance of resistance to *T. laevis* coming from Red Fife Ottawa 17 through the F_2 hybrids.

Table 18.

Parental and F_2 resistance to *T. laevis*

Parent and population numbers	Number of plants susceptible	Number of plants resistant	Percent. of plants resistant
Red Fife Ottawa 17	12	54	81.9
Garnet Ottawa 652	2	75	97.5
F_2 34-92-1	3	10	77.0
-2	0	20	100.0
-3	1	12	92.4
-4	1	13	92.9
-5	0	18	100.0
34-123-1	1	18	94.8
-2	1	16	94.2
-3	4	21	84.0
-4	0	8	100.0
-5	5	10	66.7
-6	2	17	89.5
-7	4	26	86.7
-8	1	17	94.5
Total F_2	23	206	Average 90.0 ± 2.80

From the above table it appears that some F_2 families escaped infection and that, as a whole, the percentage of susceptibility was low, consequently the factorial analysis was based on the F_3 lines only.

Table 19.

Comparative resistance of F_3 lines to *T. laevis* from Red Fife

Population numbers	Number of smutted plants	Number of non-smutted plants	Percent. of non-smutted plants	Classification
34-55-1	7	16	69.6	Susceptible
-2	0	13	100.0	Resistant
-3	4	8	66.7	Susceptible
-4	4	14	77.8	"
-5	1	13	92.9	Intermediate
-6	1	11	91.7	"
-7	2	6	75.0	Susceptible
-8	2	11	84.7	Intermediate
-9	0	14	100.0	Resistant
-10	3	14	82.4	Intermediate
-11	4	15	79.0	Susceptible
-12	1	17	94.5	Intermediate
-13	0	16	100.0	Resistant
-14	2	19	90.5	Intermediate
-15	0	12	100.0	Resistant
-16	4	17	81.0	Susceptible
34-56-1	1	10	91.0	Intermediate
-2	2	11	84.7	"
-3	2	16	88.9	"
-4	1	11	91.7	"
-5	3	21	87.5	"
-6	0	15	100.0	Resistant
-7	2	31	94.0	Intermediate
-8	6	6	50.0	Susceptible
-9	1	22	96.7	Intermediate
-10	5	15	75.0	Susceptible
-11	1	36	97.3	Intermediate
-12	6	16	72.7	Susceptible
-13	8	18	69.3	"
-15	2	13	86.7	Intermediate
-16	0	13	100.0	Resistant
-18	0	18	100.0	"
-19	0	15	100.0	"
-20	2	19	90.5	Intermediate
-21	2	18	90.0	"
-22	0	26	100.0	Resistant
-23	4	22	84.7	Intermediate
-24	1	27	96.5	"
-25	2	23	92.0	"
-26	7	21	75.0	Susceptible
-27	6	19	76.0	"
-28	2	15	88.3	Intermediate
-29	4	15	79.0	Susceptible
	105	708	Average 87.08 ± 1.76	

The F_3 lines were classified as susceptible, segregating, or resistant according to the percentage of resistance of the parents (Red Fife Ottawa 17 - 81.9 per cent.; Garnet - 97.5 per cent.). The foregoing table shows that not only the parents were highly resistant but also the F_2 families and F_3 lines. The failure to obtain a greater susceptibility is most likely due to the lowered virulence of the physiologic form of bunt used, or to its lowered efficacy in the environmental coincidence. Moreover, it may be considered that there was no difference in the germination potential of the bunt inocula since the infected heads were all harvested the same day. The standard error of a difference between means is, according to Fisher, calculated thus:

$$A - B = \sqrt{(E_1)^2 + (E_2)^2}.$$

Applying this formula, the standard error of the difference (2.92) between the means 90.0 and 87.08 of the F_2 and F_3 populations, respectively, is found to be:

$$\sqrt{(2.8)^2 + (1.76)^2} = 3.29.$$

Since the standard error of the difference is 3.29, and the difference itself is only 2.92, there can be no doubt but that the F_2 and F_3 lines are truly alike.

Table 20.

Goodness of fit of resistant, segregating and susceptible F_3 lines based on a 1 : 2 : 1 ratio.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Susceptible	13	10.75 (1)	2.25	5.06	0.4706
Segregating	21	21.50 (2)	0.50	0.25	0.0116
Resistant	9	10.75 (1)	1.75	3.06	0.2846
Total	43	43.0		x^2 =	0.7668
				P =	.5 to .7.

This is a very good fit.

The following data present the resistance of the parents, F_2 and F_3 to the *Tilletia* species derived from Garnet Ottawa 652 through the F_2 hybrid.

Table 21.

Parents and F_2 families and their reaction to *T. laevis* derived from Garnet through the F_2 generation.

Parent and population numbers	Number of smutted plants	Number of non-smutted plants	Percent. of non-smutted plants
Red Fife Ottawa 17	5	84	94.4
Garnet Ottawa 652	3	88	96.7
34-90-1	2	17	89.5
-2	0	13	100.0
-3	3	10	77.0
-4	2	19	90.5
-5	0	14	100.0
-6	3	8	72.8
34-116-1	2	16	88.9
-2	5	13	72.8
-3	1	29	96.7
Total F_2	18	139	Average 88.6 ± 3.85

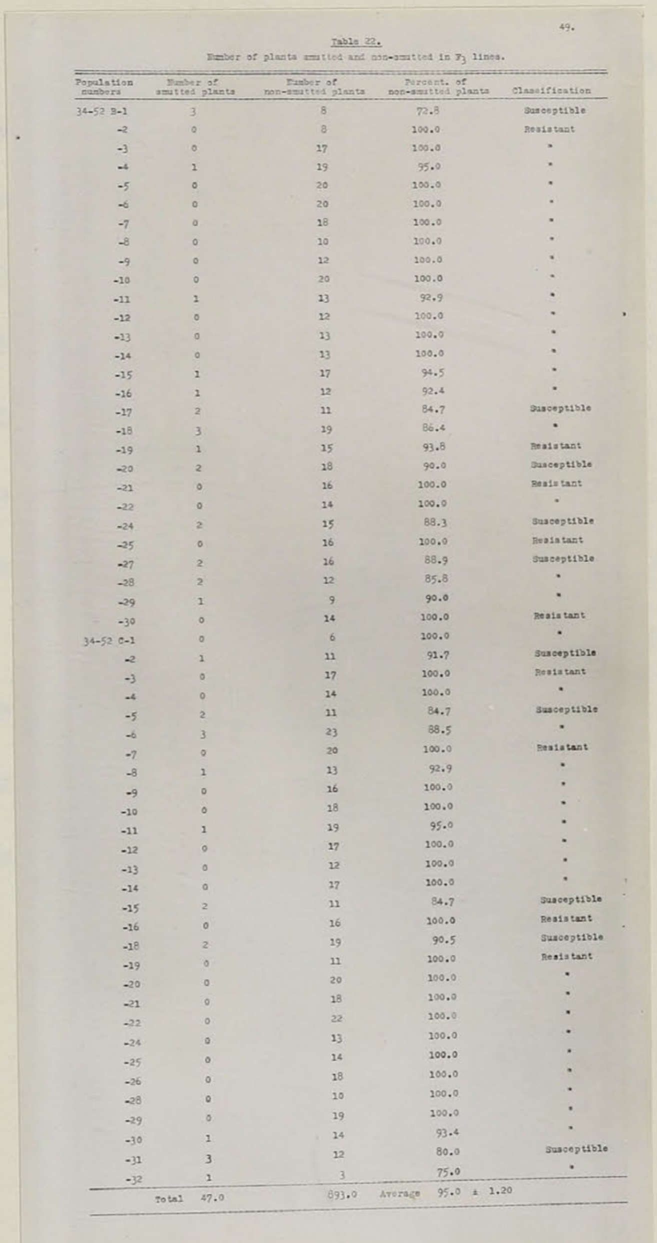

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Table 22.

Number of plants smutted and non-smutted in F_3 lines.

Population numbers	Number of smutted plants	Number of non-smutted plants	Percent. of non-smutted plants	Classification
34-52 B-1	3	8	72.8	Susceptible
-2	0	8	100.0	Resistant
-3	0	17	100.0	"
-4	1	19	95.0	"
-5	0	20	100.0	"
-6	0	20	100.0	"
-7	0	18	100.0	"
-8	0	10	100.0	"
-9	0	12	100.0	"
-10	0	20	100.0	"
-11	1	13	92.9	"
-12	0	12	100.0	"
-13	0	13	100.0	"
-14	0	13	100.0	"
-15	1	17	94.5	"
-16	1	12	92.4	"
-17	2	11	84.7	Susceptible
-18	3	19	86.4	"
-19	1	15	93.8	Resistant
-20	2	18	90.0	Susceptible
-21	0	16	100.0	Resistant
-22	0	14	100.0	"
-24	2	15	88.3	Susceptible
-25	0	16	100.0	Resistant
-27	2	16	88.9	Susceptible
-28	2	12	85.8	"
-29	1	9	90.0	"
-30	0	14	100.0	Resistant
34-52 C-1	0	6	100.0	"
-2	1	11	91.7	Susceptible
-3	0	17	100.0	Resistant
-4	0	14	100.0	"
-5	2	11	84.7	Susceptible
-6	3	23	88.5	"
-7	0	20	100.0	Resistant
-8	1	13	92.9	"
-9	0	16	100.0	"
-10	0	18	100.0	"
-11	1	19	95.0	"
-12	0	17	100.0	"
-13	0	12	100.0	"
-14	0	17	100.0	"
-15	2	11	84.7	Susceptible
-16	0	16	100.0	Resistant
-18	2	19	90.5	Susceptible
-19	0	11	100.0	Resistant
-20	0	20	100.0	"
-21	0	18	100.0	"
-22	0	22	100.0	"
-24	0	13	100.0	"
-25	0	14	100.0	"
-26	0	18	100.0	"
-28	0	10	100.0	"
-29	0	19	100.0	"
-30	1	14	93.4	"
-31	3	12	80.0	Susceptible
-32	1	3	75.0	"
Total	47.0	893.0	Average 95.0 ± 1.20	

The significant difference between the mean resistance of the F_2 and F_3 populations based on the difference of the standard error is 6.4 ± 4.03. From this it may be seen that the F_2 and F_3 lines are similar, and that it is reasonable to class all lines with less than 92 per cent. resistance as susceptible; this approximately corresponds to the mean resistance of the F_3 lines minus twice the standard error. There was a total of 59 F_3 lines, of which 35 lines were 100.0 per cent. resistant, 7 lines intermediate and 17 lines susceptible. The high resistance of the parents and F_3 lines can only be explained by assuming that the physiologic form of bunt was of low virulence and likely heterozygous for the same, and of course, that there were differences due to soil (Hanna (29)).

Table 23.

Goodness of fit of resistant, segregating and susceptible F_3 lines based on a 3 : 1 ratio.

	Observed	Calculated	O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Resistant	42	44.75 (3)	2.75	7.5625	0.1689
Susceptible	17	14.75 (1)	2.25	5.0625	0.3432
Total	59	59.0		X^2 =	.5121
				P =	.3 to .5.

It is quite probable that T. tritici from Red Fife is very similar to the form coming from Garnet, but less virulent.

The form of T. tritici coming from Garnet through the F_2 hybrid is the last one to be presented in respect of its infection capability.

Table 24.

Parents and F_2 families with their percentage resistance to *T. tritici* coming from Garnet.

Parent and population numbers	Number of smutted plants	Number of non-smutted plants	Percent. of non-smutted plants
Red Fife Ottawa 17	13	57	81.5
Garnet Ottawa 615	0	76	100.0
34-60	9	62	87.4
34-91-1	2	8	80.0
-2	1	18	94.8
34-119-1	0	9	100.0
-2	1	10	91.0
Total F_2	13	107	Average 89.2 ± 3.78

The resistance of Garnet wheat can hardly be regarded as 100.0 per cent., since one F_2 family falls in the same class.

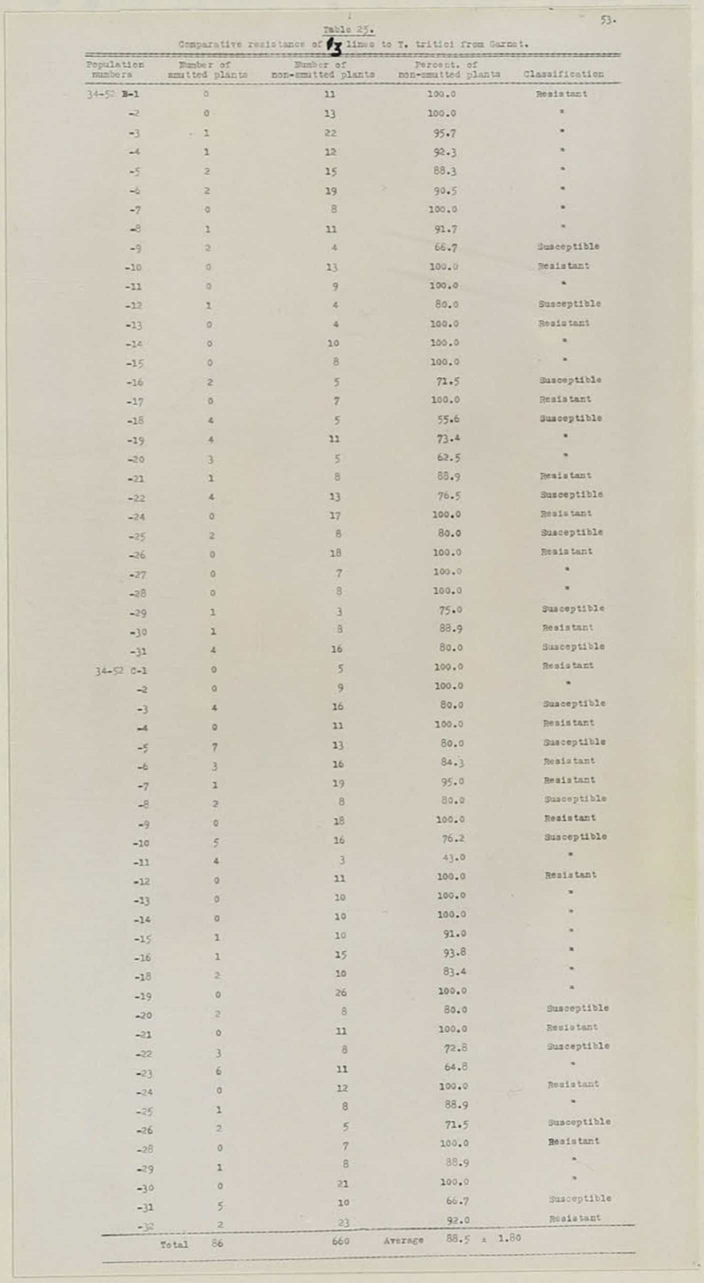

Table 25.

Comparative resistance of 13 lines to T. tritici from Garnet.

Population numbers	Number of smutted plants	Number of non-smutted plants	Percent. of non-smutted plants	Classification
34-52 B-1	0	11	100.0	Resistant
-2	0	13	100.0	"
-3	1	22	95.7	"
-4	1	12	92.3	"
-5	2	15	88.3	"
-6	2	19	90.5	"
-7	0	8	100.0	"
-8	1	11	91.7	"
-9	2	4	66.7	Susceptible
-10	0	13	100.0	Resistant
-11	0	9	100.0	"
-12	1	4	80.0	Susceptible
-13	0	4	100.0	Resistant
-14	0	10	100.0	"
-15	0	8	100.0	"
-16	2	5	71.5	Susceptible
-17	0	7	100.0	Resistant
-18	4	5	55.6	Susceptible
-19	4	11	73.4	"
-20	3	5	62.5	"
-21	1	8	88.9	Resistant
-22	4	13	76.5	Susceptible
-24	0	17	100.0	Resistant
-25	2	8	80.0	Susceptible
-26	0	18	100.0	Resistant
-27	0	7	100.0	"
-28	0	8	100.0	"
-29	1	3	75.0	Susceptible
-30	1	8	88.9	Resistant
-31	4	16	80.0	Susceptible
34-52 C-1	0	5	100.0	Resistant
-2	0	9	100.0	"
-3	4	16	80.0	Susceptible
-4	0	11	100.0	Resistant
-5	7	13	80.0	Susceptible
-6	3	16	84.3	Resistant
-7	1	19	95.0	Resistant
-8	2	8	80.0	Susceptible
-9	0	18	100.0	Resistant
-10	5	16	76.2	Susceptible
-11	4	3	43.0	"
-12	0	11	100.0	Resistant
-13	0	10	100.0	"
-14	0	10	100.0	"
-15	1	10	91.0	"
-16	1	15	93.8	"
-18	2	10	83.4	"
-19	0	26	100.0	"
-20	2	8	80.0	Susceptible
-21	0	11	100.0	Resistant
-22	3	8	72.8	Susceptible
-23	6	11	64.8	"
-24	0	12	100.0	Resistant
-25	1	8	88.9	"
-26	2	5	71.5	Susceptible
-28	0	7	100.0	Resistant
-29	1	8	88.9	"
-30	0	21	100.0	"
-31	5	10	66.7	Susceptible
-32	2	23	92.0	Resistant
Total	86	660	Average 88.5 ± 1.80	

It is quite apparent that there is no significant difference between the F_2 and F_3 average resistances, and although the variation between the families and lines is greater than twice the standard error, this must be due to differences in soil and bunt inocula. In the main, however, it seems that the bunt inocula derived from the Garnet parent are heterozygous for virulence. The susceptibility index was based on Red Fife (81.5 per cent.) and the intermediate and resistant lines bulked since the two latter could not be accurately classified.

Table 26.

Goodness of fit based on a 3 resistant : 1 susceptible hypothesis.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Resistant	40	45 (3)	5	25.0	0.6250
Susceptible	20	15 (1)	5	25.0	1.2500
Total	60	60		χ^2 =	1.875
				P =	.1 to .2.

Summary of evidence with respect to the partially dominant, single genetic factor difference for resistance and susceptibility of Garnet Ottawa 652 and Red Fife Ottawa 17, respectively, to five different sources of bunt inocula.

The various sources of the bunt inocula have given very similar results, and in three out of five cases a genetic analysis was well justified. The bunt inocula derived from Garnet Ottawa 652 were less virulent than those from Red Fife Ottawa 17. This difference in virulence is explicable on the basis of heterozygosity of the physiologic form of bunt, and consequently lessened adaptibility to the host and environmental coincidence (soil and temperature).

The total number of plants subjected to bunt in the field was:

Garnet Ottawa 652	-	382 plants
Red Fife Ottawa 17	-	355
F_2	-	682
F_3	-	3533
Total	-	4952 plants.

The partial dominance of Garnet resistance to smut, and the Red Fife susceptibility was explained on a three to one basis, and involved a population of 4952 plants. These findings are in accordance with those of Kilduff (38) who concluded that the Garnet resistance to bunt was conditioned by a single partially dominant factor. However, the question now arises: Is one justified in believing that the Garnet factor for resistance acts against both species and all forms of Tilletia, and, moreover, was there only one physiologic form of each species present? In order to obtain the correct answer to this question the following table is presented as the underlying principle for the information sought.

The simple correlation coefficient was calculated between the resistance of the F_3 lines to the inocula AB, AC and BC, according to Fisher's formula:

$$rxy = \frac{Sxy - \frac{TxTy}{N}}{\sqrt{S(x)^2 - \frac{Tx^2}{N}) \; (S(y)^2 - \frac{Ty^2}{N})}}$$

The significance was tested by obtaining the value of t.

$$t = \frac{r}{\sqrt{1 - (r)^2}} \quad x\sqrt{n - 2}.$$

The value of t is the means whereby one ascertains the probability of an occurrence due to chance alone. The greater the value of t, the smaller P becomes, and thus the smaller the chance of the result being only due to random variation. The upper limit of significance of $P = .05$.

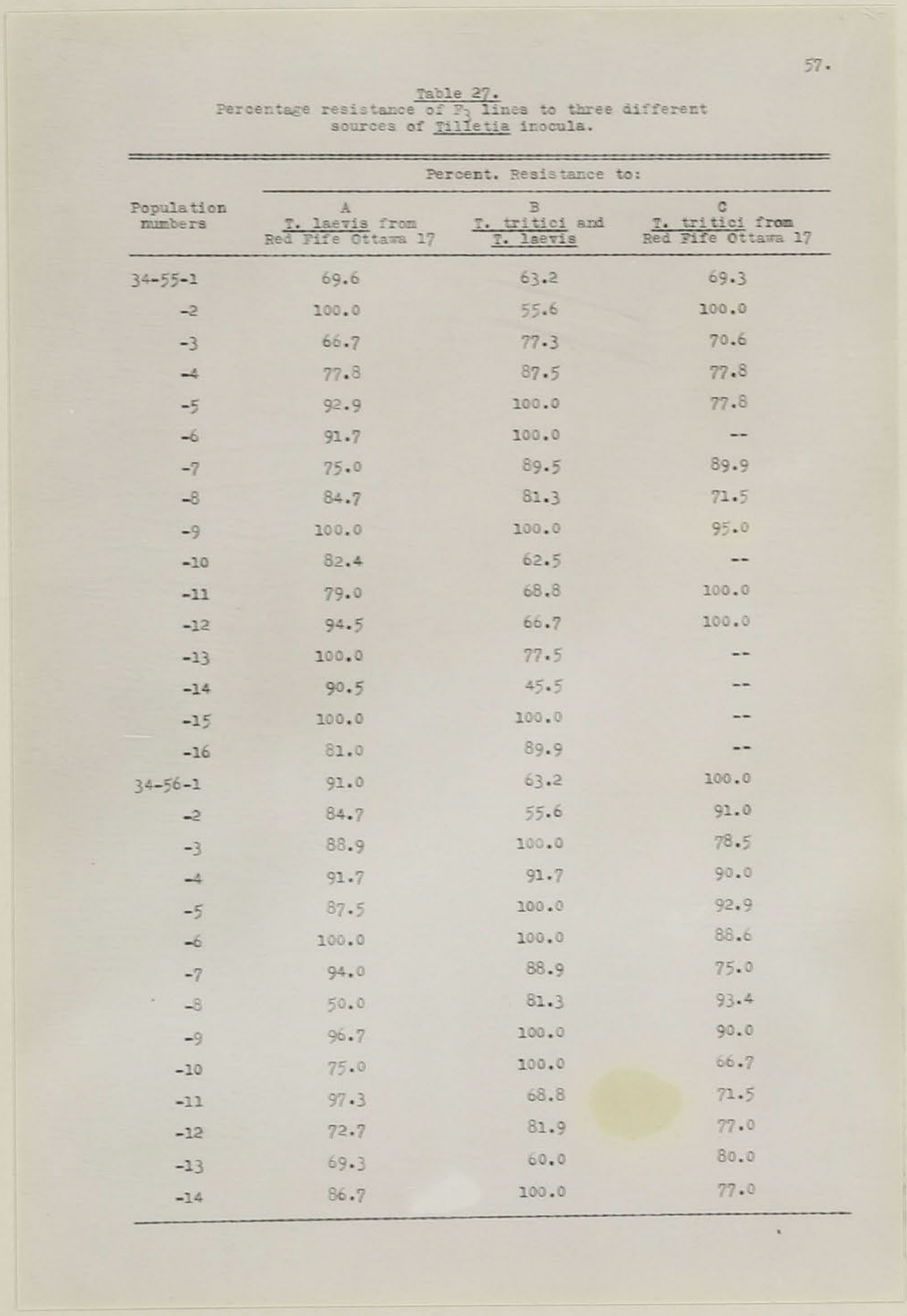

Table 27.
Percentage resistance of F_3 lines to three different sources of *Tilletia* inocula.

Population numbers	Percent. Resistance to: A *T. laevis* from Red Fife Ottawa 17	B *T. tritici* and *T. laevis*	C *T. tritici* from Red Fife Ottawa 17
34-55-1	69.6	63.2	69.3
-2	100.0	55.6	100.0
-3	66.7	77.3	70.6
-4	77.8	87.5	77.8
-5	92.9	100.0	77.8
-6	91.7	100.0	--
-7	75.0	89.5	89.9
-8	84.7	81.3	71.5
-9	100.0	100.0	95.0
-10	82.4	62.5	--
-11	79.0	68.8	100.0
-12	94.5	66.7	100.0
-13	100.0	77.5	--
-14	90.5	45.5	--
-15	100.0	100.0	--
-16	81.0	89.9	--
34-56-1	91.0	63.2	100.0
-2	84.7	55.6	91.0
-3	88.9	100.0	78.5
-4	91.7	91.7	90.0
-5	87.5	100.0	92.9
-6	100.0	100.0	88.6
-7	94.0	88.9	75.0
-8	50.0	81.3	93.4
-9	96.7	100.0	90.0
-10	75.0	100.0	66.7
-11	97.3	68.8	71.5
-12	72.7	81.9	77.0
-13	69.3	60.0	80.0
-14	86.7	100.0	77.0

Table 28.

Simple correlation coefficients for data given in tables pp.

Pairs correlated	Correlation coefficient r	Value of t	Value of P
A vs. C	.2455	1.1878	.2 to .3
B vs. C	- .2106	less	greater
A vs. B	.1724	less	greater
T. tritici ex Garnet vs. T. laevis ex Garnet	.0555	less	greater

There is no significant correlation between any of the inocula used on the F_3 lines. The inocula coming from Garnet was the least virulent and may be considered a heterozygous physiologic form of bunt having in its genotypic composition a combination of virulence factors that are common to A, B and C inocula.

Since each of the A, B, C inocula gave, singly, 3 resistant to 1 susceptible plant hybrid ratios, it is reasonable to conclude the presence of three physiologic forms of bunt, as well as three independent (complementary) factors governing resistance to them.

The genotypes of the parents and the F_1, on this basis, (see table 27), may be considered as follows:

Garnet Ottawa 652 - S_1S_1 S_2S_2 S_3S_3 - Resistant
Red Fife Ottawa 17 - s_1s_1 s_2s_2 s_3s_3 - Susceptible
F_1 - S_1s_1 S_2s_2 S_3s_3 - Partially resistant.

F_2 (phenotypes), based on segregation in the F_3:

27 $S_1S_2S_3$ - Resistant
9 $S_1S_2s_3$ - Intermediate
9 $S_1s_2S_3$ -
9 $s_1S_2S_3$ -

3 $S_1s_2s_3$
3 $s_1S_2s_3$
3 $s_1s_2S_3$ - Susceptible
1 $s_1s_2s_3$

This would give an expected F_2 ratio of: 27 resistant to 27 intermediate to 10 susceptible. The partial dominance of Garnet resistance to bunt was ascertained from the behaviour of the F_1 in the greenhouse. In addition to the three complementary factors definitely known, the type of segregation within some of the F_2 and and F_3 lines indicates the presence of modifying factors.

Table 29.

Segregation of factors for resistance to bunt in 84 F_3 lines on a tri-factorial basis.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Resistant	35	35.5 (27)	0.5	0.25	0.0070
Intermediate	31	35.5 (27)	4.5	20.25	0.5705
Susceptible	16	13.0 (10)	3.0	9.00	0.6923
Total	84	84.0 (64)		X^2 =	1.2698
This is a very good fit, for				P	.5 to .7.

The 84 F_3 lines contained a total of 1365 plants. All F_3 lines that showed less than 70.0 per cent. of infected plants were taken as susceptible, those between 70.0 and 90.0 per cent. as intermediate, and all lines above 90.0 per cent. as resistant.

C Summary.

1. Garnet Ottawa 652 and Red Fife Ottawa 17 wheat varieties proved to be resistant and susceptible to bunt, respectively.
2. The Garnet factors for resistance were found to be partially dominant in the F_1 generation.
3. No factor analysis was attempted on the greenhouse bunt experiment due to unusually favourable conditions for infection.
4. The field experiments with the various bunt inocula proved the presence of a single factor pair for resistance to each bunt form.
5. The inocula derived from Garnet wheat were of reduced virulence; this was thought to be due to heterozygosity of virulence factors in the bunt.
6. Some of the variation found in the infected F_2 families and lines was obviously due to soil heterogeneity.
7. Based on correlation, it was found that the inocula A, B, C were distinct and that corresponding genetic factors in Garnet wheat governed resistance to them.
8. The assumption of three main independent complementary factor pairs controlling the resistance of Garnet

wheat towards three physiologic forms of smut was found by the application of the X^2 test, to be correct.

5. Inheritance of Awns.

A. Review of literature.

Early genetic studies of awnedness in wheat crosses were reported by Biffen, (3) who concluded that awnless was dominant over the awned condition. Saunders (47) claimed that the F_1 of crosses between awnless and awned wheats varied in expression with varieties used. Percival (42) and Gaines and Singleton (25) obtained simple mendelian ratios for awn segregation in wheat crosses, and the latter found little, if any, linkage between awns and bunt resistance, awns and earliness.

Howard and Howard (35) were the first to study the inheritance of awnedness in hybrids of truly beardless and bearded varieties of wheat. In the F_2 they obtained five awn classes.

1. Entirely awnless
2. Short tip awns
3. Long " "
4. Nearly bearded
5. Entirely "

The grouping together of all spikes showing any signs of awns gave a dihybrid ratio of 15 awned or partially awned : 1 entirely awnless.

Harrington (30) studied the inheritance of awning in wheat hybrids, and through appropriate crosses he obtained both simple and dihybrid ratios.

The elaborate work of Stewart and Judd (52) on the inheritance of awns in wheat during five generations gave conclusive evidence of a two factor difference for awns, independently inherited.

Quisenberry and Clark (45) obtained mono- and dihybrid ratios in awn inheritance studies of Sonora wheat hybrids. Kilduff (38) working with a Garnet X Kota cross arrived at the conclusion that there was probably more than one factor involved in awn segregation of these hybrids. In addition he found linkage between the awnlet character of Garnet and bunt resistance by means of the correlation ratio, however, it was not considered to interfere greatly with breeding.

Bjaanes (4) crossed Garnet with short awns, with two Swedish and two Norwegian varieties having short awns. In every case the F_1 was bald and in the F_2 new awnless (AABB) and awned (aabb) types appeared, he concluded that Garnet carried an inhibiting factor for baldness.

The author's results bear out his conclusions with respect to awn inheritance on a two factor hypothesis (but see below).

The inheritance studies of awn characters are of great economic importance, since several authors determined an association between the awned character of wheat and yield, (Hayes (31), Goulden and Neatby (27)). On the other hand, Aamodt and Torrie (2) and Love and Chang (39), concluded that there was no association under their environmental conditions and strains of wheat investigated.

The literature on awns of wheat and its inheritance, as reviewed, stresses the significance of the use of a proper awn classification, owing to the fact that this character is often used in linkage or association tests.

B. Experimental procedure and data.

The F_2 generation of Garnet awnletted X Red Fife apical awnletted crosses were classified with respect to awns in hybrids grown in the greenhouse and in the field. The F_2 plants grown in the greenhouse were kept in definite awn classes, in order to establish the correctness of that classification in the F_3 after growing them in the field. The same field technique of planting the seeds was followed as previously outlined in this treatise.

For the awn classification a similar system to that of Clark _et al_ (12) was used, with the exception that the apical awned spikes were kept distinct from the awnless class. Thus the awn classification of the wheat spikes was:

1. Awnless, with no awnlets except a very short apical awn approximately 0.5 m.m. long.
2. Apical awnletted, awnlets from 1 to 15 m.m. long at the top.
3. Awnletted, awnlets from 3 to 40 m.m. long, the shorter ones occurring near the base of the spike and the length increasing towards the apex.
4. Awned, whenever the awns terminated the lemmas on all apikelets.

Table 30.

Goodness of fit of awn segregation in 3 F_3 families grown in the greenhouse in 1934-35.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Awnless	149	150.62 (5)	1.62	2.62	.0173
Apical Awned	151	150.62 (5)	.38	.14	.0002
Awnletted	154	150.62 (5)	3.38	11.49	.0762
Awned	28	30.14 (1)	2.14	4.57	.1516
Total	482	482.00		X^2 =	.2453

Exceedingly good fit,for P = .95 to .98

Table 31.

Goodness of fit of awn segregation in 4 F_2 families grown in the field in 1935.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Awnless	64	63.13 (5)	.87	.75	.0137
Apical Awned	63	63.13 (5)	.13	.16	.0020
Awnletted	64	63.13 (5)	.87	.75	.0137
Awned	11	12.61 (1)	1.61	2.59	.2053
Total	202	202.00		X^2 =	.2347

Exceedingly good fit, for P = .95 to .98

From tables 30 and 31 it was observed that a two factor hypothesis giving a 5 awnless : 5 apical awned : 5 awnletted : 1 awned gave a good agreement in both the greenhouse and field grown populations (4).

Table 32.

X^2 test of true breeding and segregating F_3 lines that come from F_2 families 34-52B and 34-52C.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Awnless	5	3	2	4	1.3333
Apical awned	3	3	0	0	0.0
Awnletted	4	3	1	1	.3333
Awned	3	3	0	0	0.0
Segregating	33	36	3	9	.25
Total	48	48		X^2 =	1.9166
	A very good fit, for			P =	.7 to .8

According to the data presented in tables 30, 31 and 32 the phenotypes of the parents, F_1 and F_2 are as follows:

Awnletted parent Garnet $B_1B_1b_2b_2$ X Apical awnletted Red Fife $b_1b_1B_2B_2$.

F_1 Awnless $B_1b_1B_2b_2$.

F_2 genotypes	F_3 breeding behaviour			
	Bald	Apical Awned	Awnletted	Awned
Bald (5)				
1 $B_1B_1B_2B_2$	1	0	0	0
4 $B_1b_1B_2b_2$	5	5	5	1
Apical (5)				
2 $B_1b_1B_2B_2$	1	3	0	0
1 $b_1b_1B_2B_2$	0	1	0	1
2 $b_1b_1B_2b_2$	0	3	0	1
Awnletted (5)				
2 $B_1B_1B_2b_2$	1	0	3	0
1 $B_1B_1b_2b_2$	0	0	1	0
2 $B_1b_1b_2b_2$	0	0	3	1
Awned (1)				
1 $b_1b_1b_2b_2$	0	0	0	1

For every 16 F_2 plants 4 pure breeding F_3 lines and 12 segregating F_3 lines were expected on the basis of awn types. The correctness of this assumption was given by the use of the X^2 test in table No. 32. Recently after these data were analysed it was observed that Bjaanes (4) claimed that Garnet carried one inhibitor for baldness. The author's results showed that the factors were accumulative and inhibit the expression of awns. The factors B_1 of Garnet and B_2 of Red Fife were non-allelomorphic, acted as inhibitors of awns, B_2 being more powerful than B_1.

Actually the awns of the Garnet parent are softer than those of Red Fife wheat. Previously it was stated that Kilduff (38) found linkage between the awn character of Garnet and its bunt resistance, and in view of that and its otherwise practical importance the presented investigator ascertained the number of resistant and bunted plants in each awn class in the F_3 lines of Garnet X Red Fife crosses. Since it was found that the bunt resistance of Garnet wheat was governed by three factors, the plants were classified with respect to bunt in all awn classes, and for all species and physiologic forms concerned in formulating the factorial hypothesis (table 27).. It will be recalled that each of the bunt tests gave a 3 resistant : 1 susceptible ratio.

Table 33.

F_3 lines segregating for awns and resistance to the bunt inocula T. tritici and T. laevis from the parents and F_2

Population numbers	Number of plants in awn classes.							
	Bald		Apical Awned		Awnletted		Awned	
	Resist.	Bunt.	Resist.	Bunt.	Resist.	Bunt.	Resist.	Bunt.
34-56-1	8	4	0	0	3	2	1	1
-6	21	7	0	0	0	0	0	0
-7	8	2	2	0	4	0	1	0
-8	6	1	2	2	3	0	1	0
-11	4	2	3	0	6	1	1	0
-12	5	0	1	2	2	0	1	0
-13	2	2	1	0	0	0	0	0
-14	0	0	7	3	3	2	3	1
Total	54 :	18	16 :	7	21 :	5	8 :	2

X^2's of data presented in table 33.

Bald			0.0
Apical awned			0.3617
Awnletted			0.4614
Awned			0.1333
Total	X^2	=	0.9564
	P	=	.80 to .90.

Table 34.

F_3 lines segregating for awns and resistance to the bunt inoculum T. tritici from Red Fife through the F_2.

Population numbers	Number of plants in awn classes							
	BALD		APICAL AWNED		AWNLETTED		AWNED	
	Resist.	Smutted	Resist.	Smutted	Resist.	Smutted	Resist.	Smutted
34-56-3	11	2	0	0	0	1	0	0
34-56-6	5	3	3	0	2	0	1	0
34-56-7	1	0	2	1	0	0	0	0
34-56-10	8	4	0	0	0	0	0	0
34-56-11	7	0	3	2	0	2	0	0
34-56-12	9	3	0	0	1	0	0	0
34-56-13	7	3	5	0	0	0	0	0
34-56-14	3	1	6	1	1	0	2	0
34-56-15	2	0	4	1	2	2	1	0
34-56-16	8	3	3	1	2	0	1	0
34-56-17	0	0	6	1	0	0	0	0
34-56-20	2	1	2	1	0	0	0	0
34-56-22	0	0	14	5	0	0	0	0
34-56-24	3	0	6	2	3	2	3	0
34-56-25	7	3	5	0	4	1	1	0
34-56-26	1	0	2	0	3	0	2	2
34-56-28	1	0	2	1	6	2	6	3
34-56-30	0	0	0	0	0	0	6	2
Observed	75 :	23	63 :	18	24 :	10	23 :	7

X^2's of data presented in table 34.

Bald	0.1224
Apical Awned	0.3329
Awnletted	0.3529
Awned	0.0444

Total X^2 = 0.8526

P = .80 to .90.

Table 35.

F_3 segregating lines for awns and resistance to the bunt inoculum *T. laevis* from Red Fife through the F_2.

Population numbers	Number of plants in awn classes.							
	Bald		Apical Awned		Awnletted		Awned	
	Resist.	Bunt.	Resist.	Bunted	Resist.	Bunt.	Resist.	Bunt.
34-55-1	5	1	4	1	5	4	2	1
-3	5	3	3	1	0	0	0	0
-4	4	1	6	1	2	1	2	1
-11	4	1	2	2	6	1	2	0
-16	0	0	0	0	14	3	3	1
34-56-10	11	3	4	1	0	1	0	0
-12	4	4	3	1	5	0	3	1
-13	14	3	2	3	2	1	0	0
-26	0	0	0	0	14	4	6	3
-27	0	0	0	0	0	0	19	6
	47 :	16 :	24 :	10	48 :	15	37 :	13

X^2's of data presented in table 35.

Bald	0.0052
Apical awned	0.3524
Awnletted	0.0473
Awned	0.0266

Total X^2 = 0.4315 P = .90 to .95 .

From the foregoing tables 33, 34 and 35 it was seen that the inheritance of bunt resistance in Garnet wheat was completely independent of the awn factors. In each awn group the segregation for the bunt resistance factors took place in a simple 3 resistant : 1 susceptible ratio.

C. Summary of Awn Studies

1. The F_1 of a cross between the awnletted parents Garnet and apical awnletted Red Fife was found to be awnless.
2. The F_2 segregated in a dihybrid ratio.
3. The parents carried different factors for awnlessness which behaved cumulatively in inhibiting the expression of awns.
4. It was found that the factors for smut resistance in Garnet wheat were not linked with the awn factors.

It is possible to obtain smut resistant strains of wheat in any of the desirable awn classes.

These findings are of great importance to the plant breeder.

6. Inheritance of phenol colour reactions.

A. Review of the literature.

During recent years several articles have appeared (44, 34, 43) on the use of phenol as an aid in the classification of wheat kernels of different varieties. Percival (43) and Friedberg (22, 23) claimed that the exact action of phenol upon the seed had not been ascertained. The pericarp of kernels of certain wheat varieties becomes colourless to almost black upon reacting with a solution of phenol. Friedberg (22, 23) discovered that not only the kernels produce a differential colour but also the wheat spikes of different varieties. Again, that the phenol colour characters of wheats remained very constant for the varieties were shown by the above author. Thus far, no adequate genetical evidence has been produced on the nature of the phenol colour inheritance. Fraser and Gfeller (21) followed Friedberg's work in connection with phenol colour reaction of certain Canadian wheat varieties. It was found that most of the Canadian wheats coloured similarly; however, Garnet and Red Fife wheats were distinct in respect to spike and kernel phenol colour reaction. Voss (55) observed in his work on phenol, that the kernels of wheat varieties differed in their viability, and the time required for germination under the influence of a 1 percent. solution of phenol.

B. Experimental procedure and data.

The Garnet parent was found to produce a colourless spike and dark brown kernels upon reacting with a solution of phenol, while Red Fife spike and kernel coloured dark brown and pale brown, respectively. The parents, F_1, F_2 and F_3 were grown simultaneously in the field during the summer of 1935, and after their harvest they were subjected to the phenol treatment.

The procedure of the phenol treatment is as follows: (22, 23) -

a. Spike treatment. The spike with the kernels removed is soaked for 24 hours in a 1 percent. phenol solution, then removed and dried.

b. Kernel treatment. The kernels are soaked for 16 hours in water, drained and let dry for 1 hour, then immersed in 5 c.c. of a 1 percent. phenol solution for 4 hours and dried on blotting paper. The colour is observed and recorded 4 hours after and again in 2 days after treatment.

Table 36.

F_2 families and their number of plants producing the parent range of phenol colour reactions of spikes and kernels.

Population numbers	Number of spikes and kernels in phenol colour classes.			
	Dark brown		Pale brown and colourless	
34-44 A	42	[x](48)	15	(9)
34-44 B	36	(39)	18	(15)
34-45	64	(65)	22	(21)
34-54 B	32	(34)	13	(11)
Total	174	(186)	68	(56)

Table 37.

Goodness of fit of kernel observations in table 36.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Dark brown	174	181.5 (3)	7.5	56.25	.3099
Pale "	68	60.5 (1)	7.5	56.25	.9297
Total	242	242.0		X^2 = 1.2396	
				P = .20 to .30	

---

[x] Numbers in brackets refer to the spikes.

Table 38.

Goodness of fit of spike observations in table 36.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Dark brown	186	181.5 (3)	4.5	20.25	.1115
Colourless	56	60.5 (1)	4.5	20.25	.3345
Total	242	242.0		X^2	= .4462
				P	= .30 to .50.

The X^2 shows that the assumption of a 3 dark colour : 1 light colour ratio fits both the spike and kernel phenol colour reaction hypothesis.

Table 39.

F_2 phenol colour reaction of spikes and kernels on the same plant.

	Number of plants in colour classes.		
Population numbers	Garnet colour	Garnet kernel colour Red Fife spike colour	Red Fife colour
34-44 A	9	33	15
34-44 B	15	23	16
34-45	21	44	21
34-54 B	11	22	12
Total	56	122	64

Table 40.

Goodness of fit of data presented in table 39.

	Observed	Calculated	(O-C)	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Garnet colour	56	60.5 (1)	4.5	20.25	.3345
Segregating	122	123.0 (2)	1.0	1.00	.0081
Red Fife colour	64	60.5 (1)	3.5	12.25	.2024
Total	242	242.0		X^2 =	.5452
				P =	.70 to .80.

The above observations showed that by counting the spike and kernel colours a 1 Garnet colour : 2 dominants : 1 Red Fife colour ratio was obtained.

In order to explain those results two hypotheses may be suggested:

1. The allelomorphic factor hypothesis

If this was the case Garnet and Red Fife would have different allelomorphs controlling phenol colour reaction of spikes and kernels. The genotypes would be as follows:

1. Garnet CC X Red Fife C_1C_1

F_1 CC_1

F_2 1 CC : 2 CC_1 : 1 C_1C_1

Where C results in coloured kernel and colourless spike and C_1 in pale coloured kernel and coloured spike.

2. The complete linkage of two factors:

If this was the case the genotypes would be as follows:

Garnet colourless spike (p_sp_s), dark brown kernels (P_kP_k)

Red Fife dark brown spike (P_sP_s), pale brown kernels (p_kp_k)

F_2 Dark brown spike and kernels $\overline{p_sP_k}$ $\overline{P_sp_k}$

F_2 1 $\overline{p_sP_k}\ \overline{p_sP_k}$: 2 $\overline{p_sP_k}\ \overline{p_sP_k}$: 1 $\overline{P_sp_k}\ \overline{P_sp_k}$

If the dihybrid hypothesis were correct, then one would expect a double recessive combination once out of every 16 F_2 plants. Since this did not occur in the F_2 or F_3, they must be completely linked. From the developmental genetic standpoint it is more reasonable to assume that two factors were involved, since the Garnet parent gave a colourless spike and brown kernel reactions, and Red Fife dark spike and pale kernel reactions.

Mention was made that almost all the Canadian wheat varieties gave a dark phenol colouration; and moreover, that Red Fife was the foundation wheat of all the economic important varieties, and yet all its descendants differ with respect to phenol kernel colour. From what was said, it is evident that the quality found in Red Fife wheat, was passed on irrespective of its phenol colour reaction. However, the production of new varieties differing in those colour factors will be handicapped owing to the occurrence of complete linkage.

C. Summary of phenol colouration studies.

There are two possible explanations of the inheritance of phenol colour reactions of spike and kernel : allelomorphic factors, or two completely linked factors. The latter is more plausible from the developmental standpoint.

7. General.

SUMMARY

1. The F_1, F_2 and F_3 generations of Garnet X Red Fife wheat crosses were studied with regard to the factors involved in producing earliness, bunt resistance, awns, spike and kernel phenol colour reactions.
2. Earliness of heading as found in Garnet was transmitted to the succeeding generations on a dihybrid basis, the F_1 was intermediate which suggested partial dominance.
3. In the F_3 early and late lines were represented in each of the awn classes.
4. The selection of early F_2 plants was successful in isolating this character in the F_3 lines.
5. Smut resistance of Garnet to _T._ _tritici_ (Bjerk.) Wint. and _T._ _laevis_ Kühn, to inocula coming from the latter and Red Fife bunted parent through the F_2, was found to be governed by three independent factor pairs.
6. The inheritance of awns was controlled by two cumulative, but non-allelomorphic factor pairs inhibiting the expression of awns.

7. That smut resistance of Garnet was not linked with its factors for awning was conclusively established.

8. There are two possible explanations of the inheritance of phenol colour reactions of spike and kernel : allelomorphic factors or two completely linked factors. The latter is more plausible from the developmental standpoint.

9. Garnet Ottawa 652 and Red Fife Ottawa 17 have the following genotypes in respect of inheritance of earliness, smut resistance, awns and phenol colour reaction:

Variety	Earliness	Smut Resistance	Awns	Phenol Colour
Garnet	AA bb	S_1S_1 S_2S_2 S_3S_3	B_1B_1 b_2b_2	$\overline{p_sP_k}$ $\overline{p_sP_k}$
Red Fife	aa BB	s_1s_1 s_2s_2 s_3s_3	b_1b_1 B_2B_2	$\overline{P_sp_k}$ $\overline{P_sp_k}$

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9. Literature Cited.

1. Aamodt, O.S. Varietal trials, physiologic specialization, and breeding spring wheats for resistance to *T. tritici*, and *T. laevis*. Canad. Jour. Res., 5: 501-528, 1931.

2. ____________ and Torrie, T.H. The relation between awns and yield in spring wheat. Canad. Jour. Res., 11: 207-212, 1934.

3. Biffen, R.H. Mendel's law of inheritance and wheat breeding. Jour. Agric. Sci., 1:4-48,1905.

4. Bjaanes, M. The inheritance of awns and ear colour in spring wheat. Pl. Breed. Abst.,Vol. 6, No. 2: 152, 1936.

5. Bressman, E.N. Varietal resistance, physiologic specialization, and inheritance studies in bunt of wheat. Oreg. St. Agric. Expt. Sta. Bul. 281, 1931.

6. ____________ Susceptibility and resistance of wheat varieties to bunt. Jour. Am. Soc. Agron., 24: 249-255,1932.

7. Briggs, F.N. Inheritance of resistance to bunt, *Tilletia tritici*, in wheat.
Jour. Agric. Res., 32: 973-990, 1926.

8. ______ Inheritance of the second factor for resistance to bunt, *Tilletia tritici* in Nussar wheat.
Jour. Agric. Res., 40:225-232, 1930.

9. ______ A third genetic factor for resistance to bunt *Tilletia tritici*, in wheat hybrids.
Jour. Gen., 27: 435-441, 1933.

10. Caporn, A. St. Clair An account of an experiment to determine the heredity of early and late ripening in an oat cross.
Jour. Gen., 7: 247-257, 1918.

11. Christenson, A.J. and Stakman, E.C. Physiologic specializationaand mutation in Ustilago
Phytopath., 16:979-1000, 1936.

12. Clark, J.A. and Bayles, B.B. Classification of wheat varieties grown in the United States. U.S.D.A. Tech. Bul. No. 459, 1935.

13. Crescini, F. On the behaviour of the character "earliness" in the F_2 of crosses of T. vulgare (Vill.) Pl. Breed. Abst. Vol. II, No. 3:120, 1930.

14. David, P.A. A study of crosses between Trebi and three smooth-awned varieties of barley Jour. Sci., Iowa St. Coll., 5:285-314, 1931.

15. Dillon Weston, W.A.R. Resistance of wheat varieties to bunt T. carries. Nature, 1926: 123-282, 1929.

16. Faris, S.A. Factors influencing the infection of wheat by Tilletia tritici and Tilletia laevis. Mycologia, 16:259-282, 1924.

17. Fisher, R.A. Statistical methods for research workers, 4th edition. 1932.

18. Flor, H.H. Heterothallism and hybridization in _T. tritici_ and _T. laevis_.
Jour. Agric. Res., 42: 49-58, 1932.

19. __________, Gaines, E.F. and Smith, W.K. The effect of bunt on yield of wheat.
Jour. Am. Soc. Agron., 24:778-784, 1932.

20. Florell, V.H. Studies on the inheritance of earliness in wheat.
Jour. Agric. Res., 29:333-348, 1924.

21. Fraser, J.G.C. and Gfeller, F. Two new methods of distinguishing certain Canadian wheats.
Sci. Agric., 15:564-572, 1935.

22. Friedberg, L. Essai de classification des bles d'apres leur reaction a l'acide phenique.
Annales Agronomique, 3:697-736, 1933.

23. __________ Action de l'acide phenique et de la potasse alcoolique sur la bles.
Selectionneur, Vol. 2 Fasc. 1:20-29,1933.

24. Gaines, E.F. and Smith, W.K. Reaction of varieties and hybrids of wheat to physiologic forms of bunt.
Jour. Am. Soc. Agron., 25:273-284,1933

25. Gaines, E.F. and Singleton, H.P.
Genetics of Marquis X Turkey wheat in respect to bunt resistance, winter habit and awnlessness.
Jour. Agric. Res., 32:165-183, 1926.

26. Gaudineau, Mlle. Les blés et la carie.
Selectionneur, Vol. 2, Fasc. 1:15-19, 1933.

27. Goulden, C.H. and Neatby, K.W. A study of disease resistance and other varietal characters of wheat - application of the analysis of variance, and correlation.
Sci. Agric., 9:575-586, 1929.

28. Güssow, H.T. and Conners, I.L. Smut diseases of cultivated plants.
Dom. Dept. Agric. Bul. No. 81, New Series, 1927.

29. Hanna, W.F. The physiology of the fungi causing bunt of wheat.
Pl. Breed. Abst. Vol. VI, No. 1:2, 1935.

30. Harrington, J.B. The mode of inheritance of certain characters in wheat.
Sci. Agric., 2:319-324, 1922.

31. Hayes, H.K. Inheritance of kernel and spike characters in crosses between varieties of Triticum vulgare.
Minn. Studies in Plant Sci. No. 4:163-183, 1923.

32. Heald, F.D. Manual of plant diseases, 1st Ed. 3rd Imp. McGraw-Hill Book Co. Inc. 1926.

33. ____________ and Gaines, E.F. The control of bunt or stinking smut appearing in the crop. Wash. Agric. Expt. Sta. Bul. 241.

34. Herman, W. Die Unterscheidung von Weizensorten durch Phenolfärbung der Samen. Kühn-Archiv. Bd. 19, 1928.

35. Howard, A. and Howard G.L.C. On the inheritance of some characters in wheat. Mem. Dept. Agric. India, Bot. Ser., 5:1-47, 1915.

36. Johnson, W.A. and Aamodt, O.S. The breeding of disease-resistant smooth-awned varieties of barley. Can. Jour. Res., 13:315-338, 1935.

37. Jones, W.J. Adair, C.R. Beachell, H.M. and Davis,L.L. Inheritance of earliness and length of kernel in rice. Jour. Am. Soc. Agron., 27:910-921, 1935.

38. Kilduff, T. Inheritance of bunt and loose smut reaction and of certain other characters in Kota X Bobs and Garnet crosses. Can. Jour. Res., 8:147-173, 1933.

39. Love, H.H. and Chang, R.C. A regional test of wheat. Nat. Agric. Res. Bur. Spec. Pub. No. 2: 1-38, 1934.

40. Neatby, K.W. An analysis of the inheritance of quantitative characters and linkage in barley. Sci. Agric., 9:201-218, 1929.

41. Newman, L.H. The breeding of early-ripening varieties of spring wheat in Canada. Emp. Jour. Expt. Agric., 1:1-16,1933.

42. Percival, J. The wheat plant. A monograph. Duckworth and Co., London, 1921.

43. ____________ Wheats in Great Britain, 1934.

44. Pfuhl, I.F. Die Unterscheidung der Weizensorten durch Farbung der Körner. Angew. Bot. Bd. 9 H. 3:374, 1927.

45. Quisenberry, K.S. and Clark, J.A. Inheritance of awn development in Sonora wheat crosses. Jour. Am. Soc. Agron., 25:482-492,1933.

46. Rodenhiser, H.A. and Stakman, E.C. Physiologic specialization in <u>Tilletia laevis</u> and <u>Tilletia tritici</u>.

47. Saunders, C.E. The inheritance of awns in wheat. Rept. Intern. Conf. Gen. (1906),3:370-372, 1907.

48. Smith, W.K. The two species of bunt on the same plant. Northwest Sci., 3:55-59, 1929.

49. ____________ The effect of different temperatures on the reaction of Hope wheat to bunt. Phytopath., 22:615-627, 1932.

50. ____________ Inheritance of reaction of wheat to physiologic forms of _T_. _levis_ and _T_. _tritici_. Jour. Agric. Res., 47:89-105, 1933.

51. Stephens, F.E. Inheritance of earliness in certain varieties of spring wheat. Jour. Am. Soc. Agron., 19:1060-1090, 1927.

52. Stewart, G. and Judd, B.I. Inheritance of awns in a Kota X Hard Federation cross. Jour. Am. Soc. Agron., 23:455-464, 1931.

53. Thompson, W.P. Earliness in wheat and its inheritance. Sci. Agric., 1:193-199, 1921.

54. Villiers de, P.J.R. A genetic study of the inheritance of the various characters in certain _Avena_ hybrids. Dept. Agric. South Africa, Sci. Bul. 19:1-90, 1935.

55. Voss, J. Die Unterscheidung der Weizensorten am Korn und im Laboratoriumsversuch. Biol. Reichsanstalt für land-und Forstw. H.51: 1-54, 1935.

56. Woolman, H.M. Infection phenomena and host reactions caused by *T. tritici* in susceptible and non-susceptible varieties of wheat. Phytopath., 20:637-652, 1930.

57. Zade, A. Der latente Pilzbefall und seine Folgeerscheinungen mit Bezug auf Sortenimmunität und Beizwirkung. Fortschritte der Landw., 6:388-391, 1931.

Description of Plates.

Plate I F_2 Awn types. From left to right: bald, apical awned (Red Fife type), awnletted (Garnet type), awned.

Plate II Phenol colour reactions with spikes and kernels. 1. Red Fife untreated; 2. Red Fife treated with phenol; 3. Garnet treated with phenol; 4. Garnet untreated; 5. F_1 of Red Fife X Garnet treated; 6. F_1 reciprocal; 7. F_2 Red Fife parent colour reaction; 8. Garnet and intermediate colour reaction.

Plate I

Plate II