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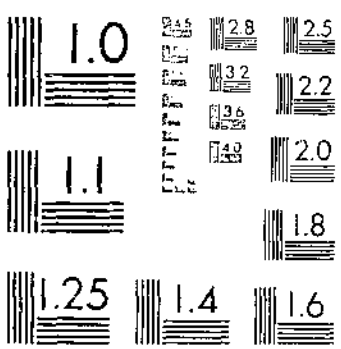
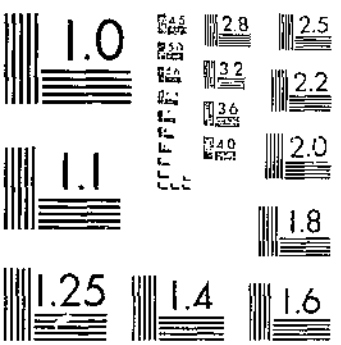


MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS 1963-A



MICROCOPY RESOLUTION TEST CHART
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INHERITANCE OF STEM-RUST REACTION AND CORRELATION OF CHARACTERS IN PENTAD, NODAK, AND AKRONA DURUM-WHEAT CROSSES[1]

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CONTENTS

INTRODUCTION

A knowledge of the inheritance and correlation of important plant and grain characters and qualities is desirable for the intelligent planning and conducting of a wheat-breeding program. An understanding of the mode of inheritance of definite characters may suggest methods to be used without wasted effort in the recovery or recombination of desirable characters. A study of the intercharacter relations is helpful in determining the effect of certain characters on other characters.

The purpose of this study was to learn more concerning the inheritance of reaction to stem rust, *Puccinia graminis* Pers., and to determine the relationships between the important contrasting characters in the three possible crosses between Pentad, Nodak, and Akrona durum wheats. The characters studied were stem-rust reaction, yield per plant, test weight per bushel, plumpness of kernel, weight of kernel, date of heading, date of ripening, length of fruiting period, gasoline color value, and protein content.

PREVIOUS INVESTIGATIONS

There have been comparatively few breeding projects and inheritance studies with durum wheat alone, but most of these have dealt with rust resistance. Much has been done in crossing *Triticum*

[1] The wheat-improvement work at the Langdon substation, Langdon, N.Dak., is carried on in cooperation with the North Dakota Agricultural Experiment Station, Fargo, N.Dak.

181892—33——1

durum Desf. and *T. vulgare* Vill.[2] in an attempt to produce common wheats that are as resistant to stem rust as are the durums.

Harrington and Aamodt (*7*) [3] reported on the seedling reaction of durum crosses to different forms of stem rust. In the greenhouse, Mindum × Pentad showed indications of a single genetic factor difference to rust form 3, and the results from form 1 also were explained by a single factor difference. These investigators obtained a continuous series of strains showing different degrees of resistance and susceptibility, but only 6 out of 110 F_3 families were strongly resistant to both forms of rust. Harrington (*6*) later reported on the inheritance of resistance to stem rust in the crosses of both Mindum and Kubanka No. 8 with Pentad; Mindum and Kubanka No. 8 were susceptible, and Pentad was resistant to rust form 34. Some of the hybrid families were found to be more susceptible than Kubanka. The results of infecting F_3 and F_4 strains of the Mindum × Pentad cross with form 34 indicated the presence of more than one factor. A different reaction was secured for Mindum × Pentad hybrids when tested to form 1 in the greenhouse than was obtained in the field. According to Harrington (*6, p. 286–287*),

> Reaction to rust was found to be inherited in the same manner as other characters. Several factors were involved, and environmental influences modified the expression of rust reaction.

In an attempt to secure a rust-resistant hard red spring wheat by crossing Marquis with Iumillo, a resistant durum, Hayes, Parker, and Kurtzweil (*9*) found they could not recover common wheats with all the resistance of the durum parent because resistance depended on several characters and factors and the numbers used were not sufficiently large. They reported a proportion of 13 susceptible plants to 1 resistant. The same writers, in reporting other *durum-vulgare* crosses, found susceptibility dominant. They concluded that the mode of inheritance for rust reaction was the same as that involved in the inheritance of botanical or morphological characters, and that a similar technic should be used in breeding for rust resistance.

Waldron (*13*) found that progenies from strains of Kubanka × Power were intermediate in their rust infection. He concluded that at least two genetic factors were responsible for rust reaction.

Puttick (*10*) explained the reaction in the F_2 generation of a cross between Marquis and Mindum to rust form 19 by a single factor plus modifiers, but a single factor did not account for the reaction to rust form 1. However, 35 out of 388 F_2 plants were resistant to both forms, indicating the possibilities of synthetic breeding for developing varieties resistant to several forms of rust.

Clark and Smith (*5*) found susceptibility to be dominant to resistance in the mature-plant stage of the durum wheat cross, Nodak × Kahla, with indications that at least two genetic factors are involved.

DESCRIPTION OF PARENTS

Pentad, or D-5, is a rust-resistant red-kerneled durum introduced from Russia in 1903 by the North Dakota Agricultural Experiment Station (*1*). The variety has white glumes and awns, and the kernels

[2] According to the rules of botanical nomenclature the name of this species is *Triticum aestivum* L., but as *T. vulgare* is in general use among agronomists, the writers give preference to that form.

[3] Italic numbers in parentheses refer to Literature Cited, p. 27.

are red, short, and plump. It was first distributed by the North Dakota station in 1911 (*4*), and since that time has been grown extensively. Farmers consider Pentad particularly desirable for late seeding, as it is not injured by rust even though sown late. However, it is of poor quality and is not desirable for the manufacture of semolina or macaroni, because the product is gray and speckled. As it brings a lower price than the amber durums it is largely used for feed or exported.

Nodak is an amber-kerneled durum which, in 1915, originated as a head selection from Kubanka (C.I.[4] no. 1440) at the Dickinson substation, Dickinson, N.Dak. (*12*). Like Pentad, it also is resistant to stem rust, though it is not equal to it in this respect. It is a high-yielding variety, especially in western North Dakota and in South Dakota, but it is undesirable in that it also produces a gray macaroni. It is not grown so extensively as Pentad.

Akrona is an amber-kerneled durum variety selected from Arnautka (C.I. no. 1493) in 1912 at the United States Dry Land Field Station, Akron, Colo. (*3*). Varietal experiments at that station showed Akrona to be the best yielding durum. It is early maturing and has a high gasoline color value, indicating suitability for the manufacture of macaroni. Under severe rust conditions, Akrona may be damaged considerably, as it is susceptible to rust. It is not commercially grown.

The contrasting differences in the characters of the three parental varieties studied that are evident under suitable environment are shown in table 1.

TABLE 1.—*Contrasting differences in the characters of Pentad, Nodak, and Akrona wheats*

Character	Contrasting differences		
	Pentad	Nodak	Akrona
Reaction to stem rust	Strongly resistant	Weakly resistant	Susceptible.
Yield	Low	High	High.
Test weight	High	Low	Low.
Plumpness	do	Medium	Do.
Weight of kernel	Light	do	Heavy.
Date of heading	Medium	Late	Early.
Date of ripening	do	do	Do.
Fruiting period	Long	Long	Long.
Gasoline color value	Very low	Low	High.
Crude-protein content	High	Medium	Low.

This experiment was planned primarily to learn more concerning the inheritance of stem-rust reaction in durum wheats. It was thought that Pentad might have the dominant immune reaction from rust similar to that of Hope common wheat (*2*). The parents seemed suited for such a study because of different degrees of rust reaction. While Pentad was not found to have the immune reaction, it is the most strongly resistant durum wheat known. Nodak is weakly resistant, and Akrona is susceptible.

Although selected primarily for differences in rust reaction, the parents exhibited marked differences in other characters, and, as shown, some of these characters were studied in the hybrid material

[4] C.I. refers to the accession number of the Division of Cereal Crops and Diseases, formerly the Office of Cereal Investigations.

in the hope that light might be thrown on the relations of such characters to each other and more particularly to rust reaction.

EXPERIMENTAL METHODS

The three crosses and their reciprocals were made at the United States Northern Great Plains Field Station, Mandan, N.Dak., in 1928. The F_1 plants were grown in a greenhouse at the Arlington Experiment Farm, Rosslyn, Va., in the winter of 1928–29, and seed from the F_1 plants was sent to Langdon, N.Dak., for sowing in the spring of 1929. No rust data were obtained on the F_1 plants.

In 1929 the F_2 population of Pentad×Nodak occupied 6 rod rows, Pentad×Akrona 5 rod rows, and Nodak×Akrona 3 rod rows, and 1 row of each parent was grown on each side of the hybrids. In 1930 the F_3 population of Pentad×Akrona occupied 150 rod rows, while of each of the other two hybrids 99 rows were grown. In 1930 the parental varieties were alternated as checks every tenth row. The kernels were spaced 3 inches apart in rod rows 1 foot apart. A row with a perfect stand contained 70 plants.

No attempt was made to introduce particular physiologic forms of stem rust nor to produce an artificial epidemic. A heavy infection was obtained by growing susceptible varieties in border rows, by spacing the seed, and by late planting. A study made by M. N. Levine, pathologist, Division of Cereal Crops and Diseases, stationed at University Farm, St. Paul, Minn., of the physiologic forms present in 1929 indicated that form 17 probably was responsible for the larger part of the infection. Rust collections made in the nursery in 1930 and sent to Levine included physiologic forms 21, 36, and 49. Inasmuch as the mature plant reactions of the parent varieties have been consistent throughout the different years, the presence or effect of different physiologic forms of stem rust was considered to be of no importance in this study.

The seasons of 1929 and 1930 were unusually favorable for developing a severe rust epidemic. In both seasons seed of these crosses was sown late, but sufficient rain prevented premature ripening. In the week following the first appearance of rust in 1930, the climatic conditions for its development were almost ideal. Very little difference was apparent in the amount of infection in the 2 years. When the relation of rust to yield is considered, however, it is apparent that rust did more damage in 1930 than in 1929.

In both years the plants were pulled when fully ripe and examined individually for rust infection. The rust reaction was quantitative in appearance, there being no distinct categories. Each plant, therefore, was classified for amount of stem rust in the following frequency classes according to the infection: 2, 10, 20, 30, 40, 50, 60, 70, and 80. These degrees of infection are illustrated in figure 1. For convenience in figuring, a trace to 4 percent was computed as 2 percent. Each percentage figure was considered the center of its class, that is, 10 was the midpoint of 5 to 14 percent, and 20 was the midpoint of 15 to 24 percent, etc.

In 1929 the parent and F_2 hybrid plants were threshed individually and the plant yields recorded. In 1930, after the rust classification was completed, the plants of each row were put together and threshed as an F_3 strain. The average yield per plant was calculated by divid-

ing the yield per row by the number of plants. Uniform stands were obtained, but a few rows were short because of lack of seed. The

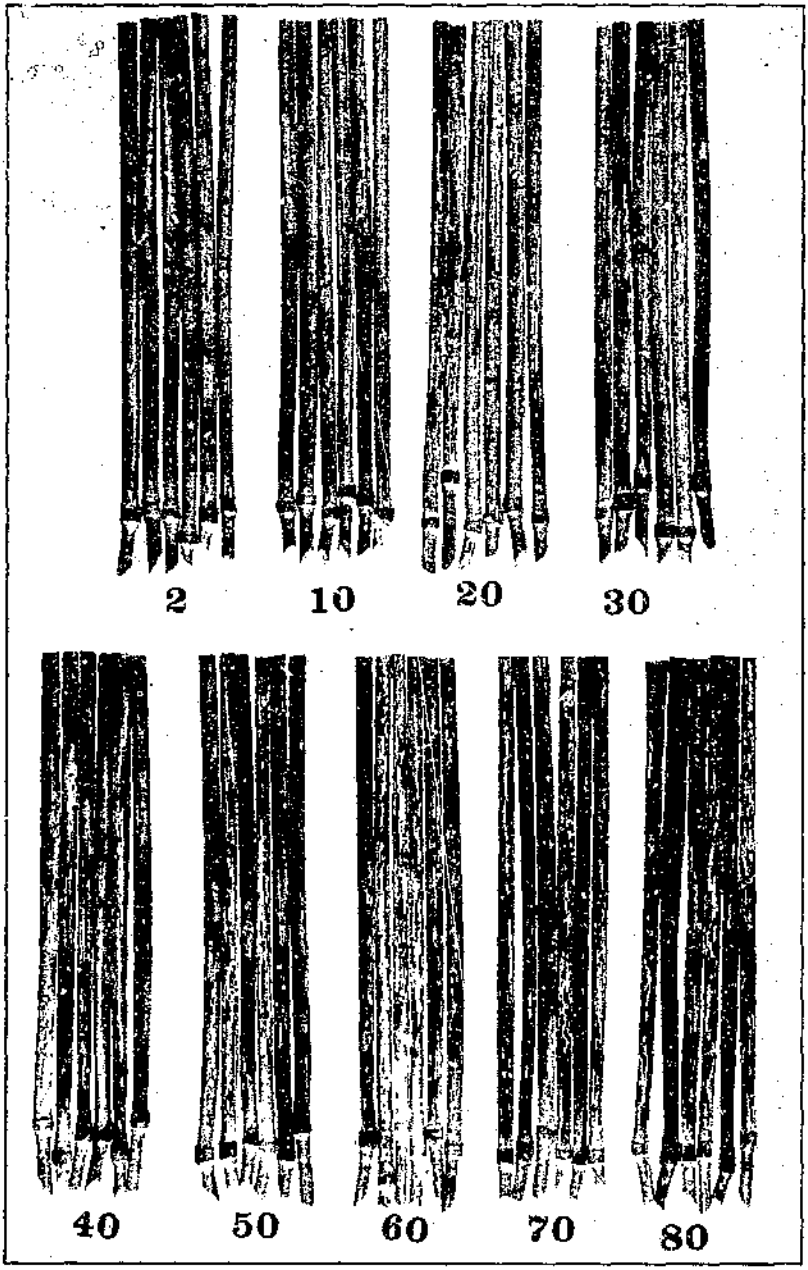

FIGURE 1.—Stem-rust infection classes used in the classification of the F_2 and F_3 generations of the triangle crosses with Pentad, Nodak, and Akrona durum wheats grown at Langdon, N.Dak., 1929 and 1930.

yield per plant was therefore more accurate than the yield per row. Test weight, kernel plumpness, weight per 1,000 kernels, gasoline

color value, and crude-protein content were determined on the grain from the F_3 strains and parent checks. Dates of heading and ripening and length of fruiting period also were noted on individual rows or strains.

SEGREGATION OF CHARACTERS

The hybrids were studied for the segregation of the various characters in comparison with the characters of the parents, in order to determine how they are inherited. The characters were all quantitative and therefore could not be classified into distinct categories, but were noted in frequency classes.

Although environmental conditions strongly influence the expression of all the characters under consideration, it seems reasonable to assume that when environmental conditions are the same for all material it should be possible to detect such inherent differences as may be present.

STEM-RUST REACTION

The inheritance of reaction to stem rust was found to be less complex than that of the other characters. For this reason the segregation of the hybrids in comparison with the reaction of the parents to stem rust will be presented separately, and that for the remaining characters will be grouped together.

PENTAD × NODAK

The segregation for stem rust of the F_2 plants of the Pentad × Nodak cross in comparison with the reaction of the parents is shown in table 2. All Pentad plants were classified in the 2 and 10 percent frequency classes, averaging 5.2 percent, and all Nodak plants in the 10, 20, and 30 percent classes, averaging 18.4 percent. None of the parent or hybrid plants were rust free or immune. Although there was overlapping of the parents, Pentad having 39.8 percent and Nodak 29.3 percent of the plants in the 10 percent class, the average difference was significant. The F_2 plants averaged 10.9 percent infection and were all distributed in the four infection classes similar to those of the parents. Because of the overlapping of parental reactions, it was not possible to separate the F_2 plants on the basis of resemblance to one or the other parent. The reaction appeared to be intermediate with no definite dominance of either strong or weak resistance. However, the average infection of the hybrids was nearer that of the strongly resistant Pentad parent.

TABLE 2.—*Segregation for stem-rust reaction of F_2 plants in comparison with the reaction of the parents, in the durum wheat cross, Pentad × Nodak, at Langdon, N.Dak., 1929*

Parent or cross	Number of rows	Number and percentage of plants by stem-rust infection class					Average percentage of rust
		2	10	20	30	Total	
Pentad:							
Number	2	53	35	------	------	88	5.2
Percentage	------	60.2	39.8	------	------	100	------
Pentad × Nodak:							
Number	6	67	127	47	15	256	10.9
Percentage	------	26.2	49.5	18.4	5.9	100	------
Nodak:							
Number	2	------	22	43	10	75	18.4
Percentage	------	------	29.3	57.4	13.3	100	------

Table 3 shows the distribution of the 99 F_3 strains of the Pentad × Nodak cross with respect to the average stem-rust infection in comparison with the average infection of the parental rows and the original F_2 behavior. By means of the reaction of the F_3 strains one may learn the breeding behavior of the F_2 plants and thereby determine to what extent the infection in F_2 was an indication of the genotype of the plant. Since the 99 strains grown in F_3 were a selected rather than a random sample of the population with reference to rust reaction, the F_2 frequency distribution has been corrected accordingly.

The parental reactions overlap in 1930 as in 1929, the average rust infections in 1930 being 7 and 10.8 percent for Pentad and Nodak, respectively; the difference, though small, is statistically significant. The infection distribution for the hybrid strains was somewhat intermediate, but the average, 9.9 percent, nearly approached that of the weakly resistant Nodak parent. This indicates segregation.

The correlation between reaction to stem rust in F_2 and F_3 is $+0.506 \pm 0.050$. (See table 14.) This value perhaps should be used with caution, because there were only four frequency classes in the F_2 distribution.

TABLE 3.—*Average stem-rust infection of 99 F_3 strains of Pentad × Nodak in comparison with that of the parents and the original and corrected F_2 frequency distribution at Langdon, N.Dak., 1929 and 1930*

Average infection for 1930	Pentad (number)	Stem-rust infection in F_3 strains grown from parents in indicated F_2 stem-rust classes								Nodak (number)	Corrected F_2 distribution (percent)
		2		10		20		30			
		Number	Percent	Number	Percent	Number	Percent	Number	Percent		
5 percent	10	7	26.9	17	39.5	3	15.8			1	29.5
10 percent	4	17	65.4	20	46.5	15	78.9	1	9.1	8	55.1
15 percent		2	7.7	5	11.6	1	5.3	6	54.5	2	12.0
Total											96.6
20 percent				1	2.4			3	27.3		2.8
25 percent								1	9.1		.6
Total											3.4
Total	14	26	100	43	100	19	100	11	100	11	100.0
	Percent	*Percent*		*Percent*		*Percent*		*Percent*		*Percent*	
Average rust in F_3	[1] 7	9		8.8		9.5		16.8		[1] 10.7	9.5
Original 1929 F_2 distribution		26.2		49.5		13.4		5.9			100.0

[1] Calculated from actual values.

On the basis of the average reaction of the strains in F_3, there were no consistent differences in the plants classified in F_2 in the 2, 10, and 20 percent rust classes. However, the plants classified as having 30 percent rust in F_2 were significantly more susceptible in F_3 than those plants in the lower frequency classes. Thus the plant reaction to stem rust in F_2 was not entirely reliable as an indicator of probable breeding behavior in F_3 for strong or weak resistance as shown in the parents. This may be due in part to difficulty in obtaining a sufficiently severe epidemic of rust in such resistant material. The

reaction to stem rust of F_3 strains suggests the genotype of the F_2 plants. In the corrected F_2 distribution 96.6 percent of the strains fell within the range of the parents, and 3.4 percent of the strains averaged higher in rust infection than did either parent. The fact that none of the hybrid plants or strains was rust free or more resistant than Pentad, the strongly resistant parent, casts some doubt on the possibility of transgressive segregation. It was evident that immunity or freedom from rust was not obtained. At the other extreme there were some F_3 plants having more rust than any of the Nodak plants, two falling in the 40 percent class, while all Nodak plants, with the exception of one with 30 percent infection, were in the lower percentage frequency classes. Of the 99 F_3 strains of Pentad × Nodak all but 17 contained plants in the 2 percent class.

The standard deviation for rust reaction was calculated for each F_3 strain and parent checkrow. These standard deviations and the average stem-rust infection are shown in table 4. The variability was not great, but 12 hybrids were more variable than any of the parent rows. This also indicates segregation, which, together with the greater amount of infection, suggests that Pentad and Nodak may differ by two minor complementary genetic factors for rust infection. Because of the small number of classes, the correlation coefficient, $+0.693 \pm 0.035$, between amount of infection and variability must be interpreted carefully, but it is apparent that the less resistant strains had the higher standard deviation. Further reference will be made to this relation in the discussion of the Pentad × Akrona cross.

TABLE. 4—*Relation between average stem-rust infection and standard deviation for rust reaction of parent checkrows and 99 F_3 strains of Pentad × Nodak grown at Langdon, N.Dak., 1930* [1]

Parent or cross and percentage of stem rust	Rows having indicated standard deviation					Total number of rows	Average percentage of rust
	2.5	3.5	4.5	5.5	6.5		
Pentad:							
5	1	7	1			9	
10		3	1	1		5	
Total	1	10	2	1		14	[2] 7.0
Hybrids:							
5		19	7	1		27	
10		12	23	16	2	52	
15			3	6	6	15	
20				1	3	4	
25					1	1	
Total		31	32	24	12	99	9.9
Nodak:							
5			1			1	
10		2	4	2		8	
15			1	1		2	
Total		2	6	3		11	[2] 10.8

[1] The solid lines around figures show the range of the parents and the dotted lines the range of both parents in comparison with the hybrids.
[2] Calculated from actual values.

The results of the studies on the Pentad × Nodak cross for degrees of rust resistance may be summarized as follows: Segregation occurred and differences were inherited in a quantitative manner; the rust reaction of the hybrids was somewhat intermediate, although the average nearly approached that of Nodak, the weakly resistant parent; in F_3 there were indications of transgressive segregation for greater infection and of more variability than had been shown by the parents. It is concluded that Pentad and Nodak may differ by two complementary minor genetic factors for stem-rust reaction, each variety apparently containing a single dominant factor for infection, and that these factors differ in amount of effect in accordance with the difference between the parents.

PENTAD × AKRONA

The parent and F_2 plants of the Pentad × Akrona cross were classified for stem-rust infection in the same manner as were those of the Pentad × Nodak cross. In 1929 the results from the progenies of five F_1 plants, including 185 F_2 plants from reciprocal crosses, were compared. As there were no apparent differences among the F_2 families, the results were combined. The number and percentage of the parent and the F_2 hybrid plants are shown in table 5. The distribution of the F_2 plants in relation to that of the parents indicates that susceptibility is partly dominant. There were 34.6 percent of the plants in the 40, 50, and 60 percent classes, which included Akrona, the susceptible parent. There were no hybrid plants in the 2 percent class and only 5.4 percent in the 10 percent class, into which 39.8 percent of the plants of Pentad, the resistant parent, were grouped. The average percentage for the F_2 hybrids, 31.6 percent, approaches the average of Akrona more closely than that of Pentad. The numbers of resistant, intermediate, and susceptible plants do not indicate a simple genetic factor difference.

TABLE 5.—*Segregation for stem-rust reaction of F_2 plants in comparison with the reaction of the parents in the durum-wheat cross, Pentad × Akrona, at Langdon, N. Dak., 1929*

Parent or cross	Number of rows	Number and percentage of plants in stem-rust class							Total	Average percentage of rust
		2	10	20	30	40	50	60		
Pentad:										
Number	2	53	35						88	5.2
Percentage		60.2	39.8						100	
Hybrids:										
Number	5		10	35	70	45	18	3	185	31.6
Percentage			5.4	18.9	41.1	24.4	8.6	1.6	100	
Akrona:										
Number	2					7	69	15	91	50.9
Percentage						7.7	75.8	16.5	100	

Of the 185 F_2 plants, 150 were chosen for further study. These were selected samples in that they contained proportionately less of the modal class and more of the extreme classes. Table 6 shows the average infection of the F_3 strains, distributed in 5 percent frequency classes and arranged according to the F_2 percentage classes, together with a corrected F_2 distribution.

Distribution of the F_3 strains shows that of 8 plants classified as having no more rust than Pentad in F_2, only 2, or 25 percent, were as resistant as Pentad in F_3. One was susceptible and evidently escaped rust infection in 1929 because of premature ripening. In this cross there was a fairly close relation between reaction to stem rust in the two generations, as shown by the correlation coefficient, which was $+0.668 \pm 0.030$. (See table 14.)

On the assumption that the genotype is more accurately indicated by the behavior of F_3 strains, the original 1929 F_2 distribution was corrected to represent a random sample of the population on the basis of the breeding behavior of the F_3 strains that were grown. The corrected F_2 distribution is suggestive of a partial dominance of susceptibility, since only 1.4 percent of the strains resembled Pentad, the resistant parent, while 16.2 percent were as susceptible as the nonresistant parent, Akrona. The average rust infection of all the F_3 strains was 31.7 percent, which, like the F_2 average, was slightly nearer the average of Akrona than to the average of Pentad.

TABLE 6.—*Average stem-rust infection of 150 F_3 strains of Pentad × Akrona in comparison with that of the parents and the original and corrected F_2 frequency distribution at Langdon, N. Dak., 1929 and 1930*

Average infection for 1930	Pentad (number)	Stem-rust infection in F_3 strains grown from parents in indicated F_2 stem-rust classes												Akrona (number)	Corrected F_2 distribution (percent)
		10		20		30		40		50		60			
		Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent		
5 percent	10														
10 percent	4	2	25.0												1.4
Total															1.4
15 percent		1	12.5	5	15.2	4	8.3								7.0
20 percent		3	37.5	11	33.3	6	12.5	2	4.7						14.6
25 percent		1	12.5	9	27.3	10	20.8	4	9.3	1	6.7				17.2
30 percent				6	18.2	18	37.5	5	11.6	2	13.3				22.8
35 percent				1	3.0	6	12.5	8	18.3	1	6.7				10.8
40 percent				1	3.0	3	6.3	10	23.2	2	13.3				10.0
Total															82.4
45 percent						1	2.1	6	14.0	4	26.7	1	33.3	4	7.1
50 percent		1	12.5					5	11.6	1	6.7	1	33.4	6	4.6
55 percent								3	7.0	4	26.6	1	33.3	4	4.5
Total															16.2
60 percent														1	
Total	14	8	100.0	33	100.0	48	100.0	43	100.0	15	100.0	3	100.0	15	100.0
	Percent	*Percent*		*Percent*		*Percent*		*Percent*		*Percent*		*Percent*		*Percent*	
Average rust in F_3	7.0	21.2		23.5		28.0		38.5		43.3		60.0		50.7	31.7
Original 1929 F_2 distribution		5.4		18.9		41.1		24.4		8.6		1.6			100.0

[1] Calculated from actual values.

The standard deviation for rust infection of each strain and parent row was calculated as before for a comparison of variability. These standard deviations and the average rust infection are shown in table 7. Most of the hybrids were much more variable than the Pentad parent, and many of them were more variable than Akrona. The

data, as a whole, indicate that the relation between rust infection and its variability is not linear, the strains intermediate for rust reaction tending to have a higher standard deviation than the resistant or the susceptible strains. This shows that the intermediate rust classes include a larger proportion of heterozygous strains than do the extreme classes.

The Akrona checkrows have a higher standard deviation than the Pentad checkrows. Akrona can scarcely be considered any less homozygous than Pentad. If a variety were immune, its standard deviation would be zero. Therefore, it appears that with increasing quantities of infection an increasing value should be taken as the maximum standard deviation consistent with homozygosity. With this in mind, a line, *xy*, was drawn in table 7, laying off the maximum standard deviation of the parents.

TABLE 7.—*Relation between average stem-rust infection and standard deviation for rust infection of parent checkrows and of 150 F_3 strains of Pentad × Akrona grown at Langdon, N.Dak., 1930* [1]

Parent or cross and percentage of stem rust	Rows having indicated standard deviation											Average deviation	Total number of rows	Average percentage of rust
	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5			
Pentad:														
5	1	8	1										10	
10		2	1	1									4	
Total	1	10	2	1								3.7	14	[2] 7
Hybrids:														
5														
10			2									4.5	2	
15				4	6							6.1	10	
20			1	6	11	3	1					6.4	22	
25			1	1	8	11	3	1			1	7.3	25	
30			1	2	9	11	2	5	1			7.5	31	
35					3	6	6	1		1		8.1	18	
40			1	1	3	4	4	2	1			7.7	16	
45					5	3	4					7.4	12	
50					1	3	3	1				8.0	8	
55					3	3	1	1				7.5	8	
60														
Total			6	14	40	43	23	11	2	1	1	7.3	150	31.7
Akrona:														
45				1	2	1							4	
50				2	1	3							6	
55				2	2								4	
60					1								1	
Total				5	6	4						6.4	15	[2] 50.7

[1] See footnote 1, table 4, for explanation of rules around figures.
[2] Calculated from actual values.

On this basis, 57 out of 150 strains may be assumed to be homozygous for their rust reactions, since their standard deviation was less than that laid off by line *xy*. This includes 38 percent of the F_3 strains and leaves 62 percent which are apparently heterozygous. Since the reaction of the F_3 strains was used to determine the genotype of the F_2 plants, these percentages refer to proportions of the F_2 population as represented by the F_3 strains. However, the F_3 strains grown were not a random sample of the F_2 population in that they contained a deficiency of strains in the 30 percent group. Since the very extreme

strains tended to be more nearly homozygous than those intermediate for rust infection, it is reasonable to expect that a strictly random sample of the F_2 population would have produced a smaller proportion of homozygous strains than was actually obtained.

According to Hayes and Garber (*8, p. 112*), two genetic factors would produce 25 percent of homozygous F_2 plants, or F_3 strains, and a single genetic factor would produce 50 percent. If, as suggested, less than 38 percent of the F_2 population were homozygous, then two genetic factors for stem rust is the most likely explanation of the reactions observed.

This arbitrary method of determining the homozygous strains is admittedly open to criticism. The homozygous and heterozygous strains probably overlap in standard deviation, and for this reason an arbitrary line cannot effect an accurate separation. However, if two dominant genetic factors for susceptibility is the essential explanation of the genetic differences in this cross, it is probable that the two factors differ in amount of effect, as evidenced by the large number of homozygous intermediate strains having different amounts of infection. The resistance of Pentad was more difficult to recover than would be expected with two simple major genetic factors. This suggests the possible presence of modifying factors.

Twenty-seven F_3 plants showing only 2 percent of rust were saved for growing as F_4 families to determine whether they were homozygous. Accordingly, in 1931 they were space-planted in rod rows, and the F_4 families were classified for stem-rust reaction. The distribution of the average infections of 27 families in the F_4 generation showed that 5 fell within a 2½ percent class, 16 in a 7½ percent class, 3 in a 12½ percent class, and 3 in a 17½ percent class.

It is significant that all of the 27 families proved comparatively homozygous for degree of resistance. The plants of the F_4 strains could always be classified in three percentage classes and generally in two. Thus the strains appeared as homozygous as standard named durum varieties. It is of further significance that most of the plant selections bred true for a comparatively strong resistance. None of the strains averaged more than 20 percent infection, and only two contained any F_4 plants with as much as 30 percent infection. Twenty-one families had an average rust infection of less than 10 percent, and these were similar to Pentad both in amount of resistance and in homozygosity.

These results show that in the Pentad × Akrona cross it is possible to recover in a homozygous condition the resistance of Pentad to stem rust.

In another test there were selected from the apparently homozygous F_3 strains four that were representative of each of the rust classes from 10 to 60 percent. A bulk sample of the seed from each was space-planted in an F_4 row in 1931, the object being to see if the strains would breed true. Pentad, Nodak, N.D.R. 216, Mindum, Akrona, and Peliss No. 14 were included for comparison. The results are summarized in table 8.

The epidemic was not so severe in 1931 as in 1930, but it is clear that there was a very definite correlation between rust reaction in F_3 and F_4. A single strain with an average of 17.7 percent infection in F_4 is a partial exception. However, it was later found that this strain was one from which eleven 2 percent plants had been selected for another

study, and thus the seed which was sown was not a random sample. Therefore, this strain was not included in the average. Pentad, Nodak, N.D.R. 216, Mindum, Akrona, and Peliss No. 14 were grown to represent different degrees of resistance and susceptibility. In comparison with the named varieties, most of the hybrid strains studied could be considered homozygous.

TABLE 8.—*Stem-rust reaction in F_4 of Pentad×Akrona strains apparently homozygous in F_3, compared with varieties with various degrees of resistance and susceptibility*

F_3 reaction classes or variety	Average F_4 strains or rows grown from parents in indicated F_3 stem-rust classes										
	5	10	15	20	25	30	35	40	45	50	Average
10 percent	2	1		[1] 1							6.4
20 percent	1	3									8.9
30 percent			3	1							16.1
40 percent					3	1					25.9
50 percent						1	2	1			35.5
60 percent							2		2		39.5
Pentad	1										3.5
Nodak	1										6.4
N.D.R. 216			1								16.1
Mindum				1							21.4
Akrona							1				36.5
Peliss No. 14										1	49.5

[1] This strain was not included in the average because it was found later that it was not a random sample.

This experiment demonstrates that F_3 strains may be obtained that are homozygous for various degrees of resistance or susceptibility intermediate between the parents.

The results of the studies on the Pentad×Akrona cross for rust reaction may be summarized as follows: The corrected F_2 reaction indicates a somewhat intermediate inheritance, although susceptibility is partially dominant; the F_2 plant reactions bore a fairly close relation to the breeding behavior of the F_3 strains; the proportion of heterozygous strains, as determined by the standard deviation for rust, suggested the presence of two major dominant genetic factors for susceptibility; it seems likely that these factors differ in amount of effect; F_4 studies showed that it is possible to recover the resistance of Pentad in a homozygous condition; homozygous F_3 strains remained constant in F_4 for different degrees of resistance and susceptibility intermediate between the parents.

NODAK × AKRONA

The Nodak×Akrona cross was handled in the same manner as the other crosses. One hundred and eleven plants were grown in F_2, and their distribution for stem-rust reaction in comparison with that of the parents is shown in table 9. An intermediate inheritance is indicated, only a single plant being found in the extremely susceptible parental rust class. The average infection of the hybrids was 34.5 percent, which is almost exactly midway between the parental averages of 18.4 percent for Nodak and 50.9 percent for Akrona. A total of 56.7 percent of the plants was included in the rust classes represented by Nodak and 43.3 percent in those represented by Akrona.

TABLE 9.—*Segregation for stem-rust reaction of F_2 plants in comparison with the reaction of the parents in the durum-wheat cross, Nodak×Akrona, at Langdon, N.Dak., 1929*

Parent or cross	Number of rows	Number and percentage of plants in the stem-rust class							Average percentage of rust
		10	20	30	40	50	60	Total	
Nodak:									
Number	2	22	43	10	----	----	----	75	18.4
Percentage	----	29.3	57.4	13.3	----	----	----	100	----
Hybrids:									
Number	3	----	11	52	36	11	1	111	34.5
Percentage	----	----	9.9	46.8	32.5	9.9	0.9	100	----
Akrona:									
Number	2	----	----	----	7	69	15	91	50.9
Percentage	----	----	----	----	7.7	75.8	16.5	100	----

TABLE 10.—*Average stem-rust infection of 99 F_3 strains of Nodak × Akrona in comparison with that of the parents and the original and corrected F_2 frequency distribution at Langdon, N.Dak., 1929 and 1930*

Average infection for 1930	Nodak (number)	Stem-rust infection in F_3 strains grown from parents in indicated F_2 stem-rust classes										Akrona (number)	Corrected F_2 distribution (percent)
		20		30		40		50		60			
		Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent		
5 percent	1	----	----	----	----	----	----	----	----	----	----	----	----
10 percent	8	----	----	1	2.0	----	----	----	----	----	----	----	0.9
15 percent	2	----	----	2	4.1	----	----	----	----	----	----	----	1.9
Total	----	----	----	----	----	----	----	----	----	----	----	----	2.8
20 percent	----	1	11.1	3	6.1	----	----	----	----	----	----	----	4.0
25 percent	----	2	22.2	----	----	----	----	----	----	----	----	----	2.2
30 percent	----	2	22.3	4	8.2	1	3.3	1	10.0	----	----	----	8.1
35 percent	----	2	22.2	7	14.3	9	30.0	----	----	----	----	----	18.6
40 percent	----	1	11.1	11	22.5	6	20.0	----	----	----	----	----	18.1
Total	----	----	----	----	----	----	----	----	----	----	----	----	51.0
45 percent	----	1	11.1	8	16.3	5	16.7	1	10.0	----	----	4	15.2
50 percent	----	----	----	8	16.3	2	6.7	1	10.0	----	----	6	10.8
55 percent	----	----	----	4	8.2	2	6.7	1	10.0	----	----	4	7.0
60 percent	----	----	----	1	2.0	2	6.7	3	30.0	1	100.0	1	7.0
Total	----	----	----	----	----	----	----	----	----	----	----	----	40.0
65 percent	----	----	----	----	----	2	6.6	----	----	----	----	----	2.2
70 percent	----	----	----	----	----	1	3.3	3	30.0	----	----	----	4.0
Total	----	----	----	----	----	----	----	----	----	----	----	----	6.2
Total	11	9	100.0	49	100.0	30	100.0	10	100.0	1	100.0	15	100.0
	Percent		*Percent*		*Percent*		*Percent*		*Percent*		*Percent*		
Average rust in F_3	[1] 10.7		31.7		39.0		44.7		57.0		60.0	[1] 50.7	42.4
Original 1929 F_2 distribution	----		9.9		46.8		32.5		9.9		.9	----	100.0

[1] Calculated from actual values.

Only 99 F_2 plants were selected for growing as F_3 strains. The average stem-rust infection in F_3 as compared with the F_2 plant reaction is shown in table 10. The correlation coefficient for reaction of F_2 plants and the average infection of F_3 strains was $+0.472 \pm 0.053$. (See table 14.) This is not so high as the corresponding coefficients for the two crosses previously discussed, but doubtless there was a direct relation. The corrected F_2 distribution shows that 2.8 percent of the plants were similar to Nodak in their reaction,

51 percent were intermediate between the parents, 40 percent were similar to Akrona, and 6.2 percent averaged more than Akrona, the susceptible parent. This again suggests transgressive segregation for stem-rust infection, but no further evidence is available since no strains of this cross were tested in F_4. Two major genetic-factor differences are strongly indicated. However, the difficulty of recovering strains resembling the weak resistance of the Nodak parent suggests the presence of the two minor factors of the Pentad × Nodak cross or additional modifying factors.

The standard deviations for rust reaction of each strain and parental row were also calculated for this cross and are shown in table 11. Ninety of the ninety-nine hybrid strains had a higher standard deviation than Nodak, and fifty-two had a higher standard deviation than Akrona. The susceptible parent again had a higher standard deviation than the resistant parent, and for this reason the method explained in the Pentad × Akrona cross was used to lay off arbitrarily the maximum standard deviation in the hybrids consistent with homozygosity. On this basis, 30½ strains, or 30.8 percent, were comparatively homozygous for stem-rust reaction. Probably these strains include a few near the border line that are not entirely homozygous. If a single factor for rust reaction were present, 50 percent of the strains should have been as homozygous as the parents. Therefore, if the standard deviations are a fair indication of the heterozygosity of the strains, at least two genetic factors are necessary to explain the inheritance of rust reaction.

TABLE 11.—*Relation between average stem-rust infection and standard deviation of parent checkrows and 99 F_3 strains of Nodak × Akrona grown at Langdon, N. Dak., 1930* [1]

Parent or cross and percentage stem rust	Rows having indicated standard deviation											Average	Total number of rows	Average percentage of rust
	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5			
Nodak:														
5		1											1	
10	2	4	2										8	
15		1	1										2	
Total	2	6	3									4.6	11	[2] 10.7
Hybrids:														
5														
10			1									5.5	1	
15			1	1								6.0	2	
20		1		2	1							6.3	4	
25				1			1					8.0	2	
30					4	2	1	1				8.4	8	
35				2	4	4	5	2			1	8.8	18	
40		1		1	5	3	3	3			1	8.7	17	
45			1	1	3	5	2	1	3			8.7	16	
50				2		3	3	2		1		9.1	11	
55			1	1	2		1	1	1			8.4	7	
60			2	1	3				1			7.4	7	
65			1		1	1						7.2	3	
70				3			3					6.5	3	
Total		2	7	15	23	18	16	10	5	1	2	8.3	99	42.35
Akrona:														
45			1	2	1								4	
50			2	1	3								6	
55			2	2									4	
60				1									1	
Total			5	6	4							6.4	15	[2] 50.7

[1] See footnote 1, table 4, for explanation of rules around figures. [2] Calculated from actual values.

The average standard deviation for groups of strains in the respective rust classes increases in value with the heavier infections until the classes are reached containing the Akrona parents, when it decreases. In this cross very few intermediate strains appear homozygous. This indicates that more genetic factors are involved than in the Pentad × Akrona cross. That susceptibility to rust is partly dominant is further indicated by the number of the heterozygous strains that average as high as Akrona.

The results of the studies on the Nodak × Akrona cross for stem-rust reaction may be summarized as follows: The reaction of the F_2 plants was only a fair indication of the breeding behavior of the F_3 strains; susceptibility was partly dominant to resistance; evidence of transgressive segregation was more pronounced than in the Pentad × Nodak cross, as already discussed; the proportion of homozygous strains, as measured by the standard deviations, indicates that the parents may differ by two major genetic factors. The difficulty of recovering strains resembling the resistant parent, and the fewer homozygous intermediate strains, suggest the presence of the two minor factors of the Pentad × Nodak cross or additional modifying factors.

SUMMARY OF THE THREE CROSSES

The results of the studies of stem-rust reaction in the three crosses are summarized in table 12 and are shown graphically in figure 2. The data show that rust reaction was inherited in a quantitative manner and that no rust-free or immune plants were obtained. The strong resistance of Pentad was not inherited as a dominant character, as was the near immunity of Hope. The different degrees of resistance of both the Pentad and Nodak parents were inherited as recessive characters in crosses with the susceptible Akrona. The resistance of the parents was recovered in the hybrids, although more resistance than that of the resistant parent was not obtained.

TABLE 12.—*Summary of stem-rust infection of parents and the corrected F_2 frequency distribution of 3 wheat crosses, at Langdon, N. Dak., 1930*

Percentage of stem rust	Percentage of plants of parent or cross					
	Pentad	Nodak	Akrona	Pentad × Nodak	Pentad × Akrona	Nodak × Akrona
5	71.4	9.1		29.5		
10	28.6	72.7		55.1	1.4	0.9
15		18.2		12.0	7.0	1.9
Total				96.6	8.4	2.8
20				2.8	14.6	4.0
25				.6	17.2	2.2
30					22.8	8.1
35					10.8	18.6
40					10.0	18.1
Total				3.4	75.4	51.0
45			26.7		7.1	15.2
50			40.0		4.6	10.8
55			26.7		4.5	7.0
60			6.6			7.0
Total					16.2	40.0
65						2.2
70						4.0
Total						6.2
Average	7.0	10.7	50.7	9.5	31.7	42.4

A somewhat intermediate inheritance was shown in the Pentad × Nodak cross between strong and weak resistance, although the average more nearly approached that of Nodak, the weakly resistant parent. There was evidence of transgressive segregation for a greater infection.

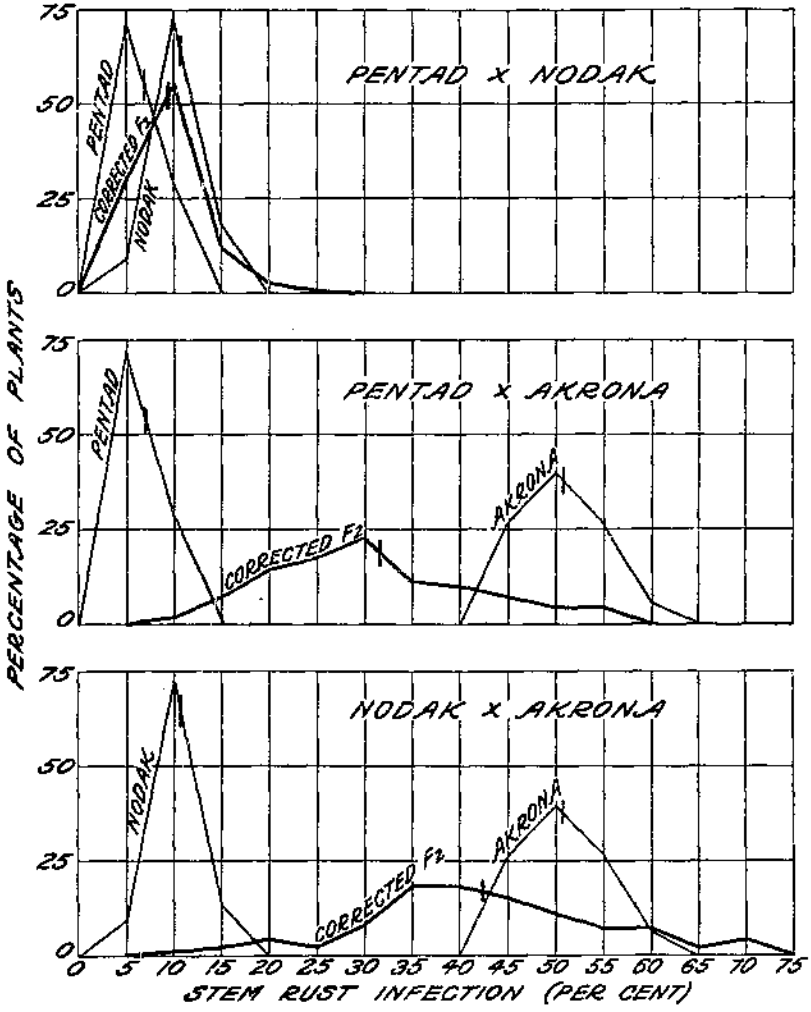

FIGURE 2.—Frequency distribution of the corrected F_2 of three wheat crosses and the parents, together with their average infection, at Langdon, N.Dak., 1930.

Pentad and Nodak appear to differ by at least two minor genetic factors, each variety apparently carrying a single dominant factor for infection which differs in amount of effect, in accordance with the difference between the parents.

The Pentad × Akrona cross revealed that susceptibility was incompletely or partly dominant and that the parents appeared to differ by at least two major factors, Akrona carrying both dominant susceptible factors.

The Nodak × Akrona cross more strongly revealed susceptibility partly dominant to resistance. Two major genetic factor differences are indicated. Transgressive segregation was obtained for a greater infection and was more pronounced than in the Pentad × Nodak cross. This, together with the difficulty of recovering the weak resistance of the Nodak parent and the fewer number of intermediate homozygous hybrid strains than in the Pentad × Akrona cross, suggests the presence of the two minor factors of the Pentad × Nodak cross or additional modifying factors.

Any genetic interpretation of the results for the three crosses must be based upon the assumption that susceptibility is partly dominant and that several genetic factors are involved. The factors may all differ in amount of effect. Two minor factors appear to account for inherent differences between the strong resistance of Pentad and the weak resistance of Nodak. Two major factors appear to separate the susceptible Akrona from the resistant Pentad. At least 2 major and possibly 2 minor factors appear to separate the Nodak and Akrona parents. It is recognized that these are not factors for rust, as such, but rather are factors controlling morphologic or physiologic responses of the plant, the expression of which appears as rust infection.

OTHER CHARACTERS

Inasmuch as segregation of the hybrids for quantitative characters other than stem-rust reaction did not furnish data which could be interpreted to show their method of inheritance, this discussion will be limited to a summary of the average results. The number of plants studied, the mean, and the standard deviation for each of the characters of the F_3 hybrids and the parents, so far as they are available, are presented in table 13.

Inheritance of reaction to stem rust has been discussed, but before proceeding with the other characters it is important to note the average values for rust infection that have a bearing on the differences in other character means. Pentad is strongly resistant, averaging 7.1 percent of rust infection, while Nodak is weakly resistant, averaging 10.8 percent. Akrona is susceptible, averaging 50.7 percent infection. The hybrids in each case carry an average stem-rust infection somewhat intermediate between the parents. The Nodak × Akrona cross was significantly more susceptible than the Pentad × Akrona cross. It also is shown that the variability, as measured by the standard deviation, was high as compared with that of the parents in crosses with Akrona, while but little more variability was shown by the cross between Pentad and Nodak than by the parents in segregation for rust reaction.

TABLE 13.—*Number, mean, and standard deviation of row-mean distributions for the characters studied on F_3 strains and parents of the triangle crosses with Pentad, Nodak, and Akrona durum wheats at Langdon, N. Dak., 1930*

Characters	Pentad × Nodak			Pentad × Akrona			Nodak × Akrona			Pentad			Nodak			Akrona		
	Number	Mean	Standard deviation	Number	Mean	Standard deviation	Number	Mean	Standard deviation	Number	Mean	Standard deviation	Number	Mean	Standard deviation	Number	Mean	Standard deviation
Stem rust	99			150			99			14			11			15		
Percent		9.6	3.9		31.7	11.1		42.4	12.2		7.1	1.7		10.5	2.1		50.7	4.0
Plant yield	99			150			99			14			11			15		
Grams		4.5	.5		3.7	.7		2.4	1.0		4.4	.7		3.7	.7		2.4	.7
Test weight	88			72						12			8					
Pounds per bushel		58.6	.8		58.3	1.1					58.8	.4		57.8	.7			
Plumpness	99			144			71			14			11			8		
Percent		80.3	3.2		77.9	7.4		72.3	7.1		85.4	2.3		80.5	1.5		61.9	7.5
Kernel weight	99			142			71			14			11			8		
Grams		35.6	1.3		36.5	2.8		30.9	3.9		36.7	1.2		32.5	1.8		28.9	7.2
Heading	99			150			99			14			11			15		
Date (July)		17.5	1.1		15.9	1.1		18.3	1.8		17.1	.6		17.5	1.0		16.1	1.2
Ripening	99			150			99			14			11			15		
Date (August)		25.8	.5		20.4	1.2		23.6	1.3		23.0	2.2		25.1	1.4		20.5	1.5
Fruiting period	99			150			99			14			11			15		
Days		39.3	1.0		35.5	1.4		36.5	1.7		36.9	1.8		38.3	1.5		35.4	1.2
Gasoline color	98			150			97			14			11			15		
Value		.6	.1		1.3	.3		.4	.2		.7	.2		.6	.1		1.8	.2
Protein	99			149			96			14			11			15		
Percent		14.8	.4		14.1	.7		14.6	.9		15.0	.4		14.7	.6		13.7	.5

The average yields per plant were in inverse relation to the stem-rust infections. Pentad was the highest yielding parent, averaging 4.4 g per plant, Nodak averaged 3.7 g per plant, and Akrona averaged 2.4 g. Pentad × Nodak, the most resistant cross, yielded 4.5 g per plant, the Pentad × Akrona cross yielded 3.7 g, and Nodak × Akrona, the most susceptible cross, yielded 2.4 g per plant. The yields of Pentad × Nodak cross were the least variable, while those of Nodak × Akrona were the most variable, which might be expected from the respective effects of rust in the three crosses. The standard deviations of the parents were alike within the limits of random errors.

The results for test weight per bushel are incomplete because of inability to obtain weights on the Akrona parent, the Nodak × Akrona strains, and on some of the Pentad × Akrona strains. The Pentad parent averaged 58.8 pounds per bushel, which is significantly higher than that of Nodak, averaging 57.8 pounds.

Pentad had the plumpest kernels, averaging 85.4 percent, while those of Nodak averaged 80.5 and those of Akrona averaged 61.9 percent. Akrona was much more variable in plumpness than either Pentad or Nodak, and this variability probably is the result of the more variable rust infection of Akrona.

The mean and the standard deviation for the hybrids were also in inverse relation to the average rust infections. The Akrona rows also were high in variability of mean kernel weight, which is another measure of plumpness. The parents varied inversely for kernel weight in relation to stem rust, as would be expected. Thus Pentad averaged 36.7 g per 1,000 kernels, Nodak 32.5, and Akrona 28.9. Size and specific density of kernel, as well as the shriveling caused by rust, enter into this character. The hybrids were intermediate between the parents in this respect, but the average weight of the kernels of Pentad × Akrona was nearly as much as that of the kernels

of Pentad. Many of the Pentad × Akrona strains had heavier kernels than those of Pentad.

Akrona was earlier in heading and ripening and shorter in fruiting period than either of the other parents. The two crosses of Pentad and Nodak with Akrona were significantly shorter in fruiting period than the Pentad × Nodak cross. Correlations discussed later indicated that this was not caused by their greater susceptibility to stem rust.

In gasoline color value, Pentad and Nodak were very low, while Akrona was high. Nodak has generally been thought to carry more yellow color than Pentad, but the results here reported show Pentad to be slightly higher in color value, the difference being barely significant. Moreover, this difference in the parents was borne out by a comparison of the average gasoline color values for the hybrids of Pentad and Nodak with Akrona. The Pentad × Akrona strains averaged significantly higher than the Nodak × Akrona strains, and the Pentad × Nodak material, of course, was very low in color value. The distribution of the hybrid strains in comparison with that of the parents showed a tendency for low content of carotin to be dominant.

Of the parents, Pentad was the highest in protein content, averaging 15 percent; Nodak averaged 14.7 and Akrona 13.7 percent. In each case the average for the hybrids was intermediate between that of the parents. The Nodak × Akrona strains averaged significantly higher than the Pentad × Akrona strains, in spite of the fact that the Pentad parent was significantly higher in protein than Nodak. Because of the complex nature of these characters, it was not possible to draw more specific conclusions as to the nature of their inheritance, but this summary of the results should be important in suggesting how and to what extent these characters are inherited.

CORRELATION OF CHARACTERS

Correlation coefficients were calculated for the possible pairs of characters studied by using the mean character values for each F_3 strain and the F_2 plant reaction in the case of stem rust. These coefficients are shown in table 14. Certain partial correlations also were determined and are mentioned in the text wherever they throw further light on the relations.

TABLE 14.—*Simple correlations of characters in the triangle crosses with Pentad, Nodak, and Akrona durum wheats at Langdon, N. Dak., 1930*

Characters correlated	With average stem rust per F_3 strain [1]								
	Pentad × Nodak			Pentad × Akrona			Nodak × Akrona		
	Number	r	P.E.r	Number	r	P.E.r	Number	r	P.E.r
Average stem rust of F_3 strains:									
Rust per F_2 plant	99	**+0.508±0.050**		150	**+0.668±0.030**		99	**+0.472±0.053**	
Average yield per F_3 plant	99	−.085± .067		150	**−.332± .049**		99	**−.625± .041**	
Test weight of F_3 strain	88	−.269± .069		72	**−.430± .065**				
Plumpness, percent				144	**−.502± .042**		71	**−.505± .060**	
Weight per 1,000 kernels	99	−.147± .066		142	**−.494± .043**		71	**−.757± .040**	
Heading date per strain	99	+.147± .066		150	**+.122± .054**		99	**+.031± .067**	
Ripening date of strain				150	−.014± .055		99	−.151± .066	
Fruiting period	99	+.075± .067		150	−.126± .054		99	−.168± .066	
Gasoline color value	98	−.002± .068		150	**+.082± .054**		97	**+.170± .067**	
Protein content, percent	99	−.278± .063		149	**−.364± .048**		96	**−.277± .064**	

[1] The statistically significant values are shown in boldface type.

TABLE 14.—*Simple correlations of characters in the triangle crosses with Pentad, Nodak, and Akrona durum wheats at Langdon, N.Dak., 1930*—Continued

Characters correlated	With average stem rust per F_3 strain								
	Pentad × Nodak			Pentad × Akrona			Nodak × Akrona		
	Number	r	P.E.r	Number	r	P.E.r	Number	r	P.E.r
Average yield per F_3 plant:									
Test weight of strain	88	+0.095±0.071		71	+0.232±0.075				
Plumpness, percent				144	+ .452± .045		71	+0.645±0.047	
Weight per 1,000 kernels	99	+ .295± .062		142	+ .452± .045		71	+ .334± .071	
Heading date	99	− .328± .061		150	− .241± .052		99	− .295± .062	
Ripening date				150	+ .232± .053		99	+ .299± .062	
Fruiting period	99	+ .337± .060		150	+ .394± .046		97	+ .505± .067	
Gasoline color value	98	− .070± .068		150	+ .031± .055		97	− .155± .067	
Protein content, percent	99	+ .210± .065		149	+ .011± .055		98	+ .032± .069	
Test weight per bushel:									
Plumpness, percent				72	+ .627± .048				
Weight per 1,000 kernels	88	+ .087± .071		72	+ .468± .062				
Heading date	88	− .178± .070		72	− .251± .074				
Ripening date	88			72	+ .226± .075				
Fruiting period	88	+ .104± .071		72	+ .388± .067				
Gasoline color value	87	+ .000± .072		72	− .190± .076				
Protein content, percent	88	+ .172± .070		71	+ .026± .080				
Plumpness of kernel:									
Weight per 1,000 kernels				142	+ .835± .034		71	+ .756± .034	
Heading date				144	− .093± .056		71	− .138± .078	
Ripening date				144	+ .124± .055		71	+ .259± .075	
Fruiting period				144	+ .108± .055		71	+ .323± .072	
Gasoline color value				144	− .019± .056		71	− .161± .078	
Protein content, percent				143	+ .082± .056		71	+ .021± .080	
Weight per 1,000 kernels:									
Heading date	99	− .216± .065		142	− .230± .053		71	− .086± .070	
Ripening date	98			142	+ .159± .055		71	+ .091± .079	
Fruiting period	99	+ .275± .063		142	+ .378± .049		71	+ .141± .078	
Gasoline color value	98	+ .095± .068		142	+ .070± .057		71	− .134± .078	
Protein content, percent	99	− .236± .064		141	+ .184± .055		71	+ .175± .078	
Date of heading:									
Date of ripening				150	+ .319± .050		99	+ .326± .061	
Gasoline color value	98	+ .237± .064		150	+ .068± .055		97	+ .004± .068	
Protein content, percent	99	+ .124± .067		149	− .238± .052		98	+ .220± .065	
Date of ripening:									
Gasoline color value				150	− .183± .053		97	− .025± .068	
Protein content, percent				149	− .247± .052		96	+ .042± .068	
Fruiting period:									
Gasoline color value	98	− .291± .062		150	− .208± .053		97	− .135± .067	
Protein content, percent	99	− .112± .066		149	− .022± .055		96	− .272± .064	
Gasoline color value:									
Protein content, percent	98	+ .090± .068		149	− .156± .054		98	− .281± .064	

STEM-RUST REACTION AND OTHER CHARACTERS

As previously noted, the coefficients for the stem-rust reaction in F_2 and those in F_3 for the strains of Pentad × Nodak were $+0.506 \pm 0.050$; for those of Pentad × Akrona, $+0.668 \pm 0.030$; and for those of Nodak × Akrona, $+0.472 \pm 0.053$.

As would be expected, the relation of yield to rust depends upon the susceptibility of the hybrids. Thus, an insignificant coefficient, -0.085 ± 0.067, was obtained for the Pentad × Nodak strains, whereas those for the Pentad × Akrona strains and the Nodak × Akrona strains were -0.332 ± 0.049 and -0.625 ± 0.041, respectively. These coefficients were not affected significantly by eliminating by means of partial correlation coefficients the effect of the fruiting period, the most important other factor studied in relation to yield.

Rust also reduced the test weight, as evidenced by the correlation coefficients of -0.209 ± 0.069 for the Pentad × Nodak strains and -0.430 ± 0.065 for the Pentad × Akrona strains. Most of the Nodak × Akrona strains were so injured by rust that they did not

produce sufficient grain for test-weight determinations, but the coefficient, if available, would no doubt have been high and negative.

Because of the small range in plumpness of strains of Pentad × Nodak, correlation coefficients with plumpness were not warranted nor significant. That rust decreased the plumpness of kernel is indicated by the negative correlation coefficients, -0.502 ± 0.042 for the Pentad × Akrona strains and -0.505 ± 0.060 for the Nodak × Akrona strains.

Weight of kernel was another character severely affected by stem rust. The coefficients are -0.147 ± 0.066 for the Pentad × Nodak strains, -0.494 ± 0.043 for the Pentad × Akrona strains, and -0.757 ± 0.046 for the Nodak × Akrona strains, being in each case slightly higher than the corresponding coefficients for yield.

The more susceptible strains also tended to be lower in protein content, the coefficients being -0.278 ± 0.063 for the Pentad × Nodak cross, -0.364 ± 0.048 for the Pentad × Akrona hybrids, and -0.277 ± 0.064 for the Nodak × Akrona progenies. This relation between protein content and rust infection may appear contradictory to the generally accepted idea that shriveled grain is higher in protein content than plump grain. Shollenberger and Kyle (*11*) found, however, that the relation between protein and test weight is curvilinear. They found that in samples weighing more than 53 pounds a bushel the correlation between test weight and protein was negative, while in samples weighing less than 53 pounds a bushel the correlation was positive. They observed that test weights under 53 pounds were rarely found except under conditions of severe rust, and concluded that rust was responsible for the lowering of protein in those cases. The lowering of test weights to about the 53-pound level was attributed to lack of moisture, which arrests growth and shortens the fruiting period. It would appear in the Pentad × Akrona cross that rust rather than moisture was the limiting factor, and hence the negative correlation between rust and protein agrees with the results cited. Possibly nitrogenous compounds, either intended for the kernel or already stored in it, are appropriated as food by the rust fungus before they have been transformed into the final stage of protein in the kernel.

Heading and ripening dates, fruiting period, and gasoline color values were not consistently related to rust reaction.

YIELD AND OTHER CHARACTERS

The average yield per F_3 plant and test weight per bushel were not closely related in the Pentad × Nodak strains, but in the Pentad × Akrona strains the correlation coefficient was $+0.232 \pm 0.075$. A partial coefficient eliminating the effects of rust and fruiting period reduced the value to -0.029 ± 0.079. This indicates that the relation between yield and test weight was due to the dependency of both characters on rust infection and fruiting period, chiefly the former.

Yield and plumpness were rather closely associated. Thus in the Pentad × Akrona strains the correlation coefficient was $+0.452 \pm 0.045$, and in the Nodak × Akrona strains it was $+0.643 \pm 0.047$. The values were somewhat reduced by eliminating the effect of rust, but they were not significantly changed by holding constant the effect of fruiting period. The magnitude of the net correlations suggests

that plumpness may be considered a fairly reliable index of the probable yielding ability of any durum-wheat strain regardless of variations in rust reaction or in length of fruiting period.

As would be expected from the previous observations, the yield per plant also was positively correlated with kernel weight. Partial correlation coefficients indicated that stem rust and fruiting period played somewhat greater parts in this relation than in the relation between yield and plumpness, but nevertheless it seemed that kernel weight might be an important index to the probable yielding ability of new strains.

Yield was negatively associated with date of heading. The earlier a strain headed, the higher it tended to yield. In each case the partial correlation, holding constant the effect of ripening, gave a value higher than that of the simple correlations.

Date of ripening was positively correlated with yield, the later ripening strains tending to be the higher yielding. These values were greater when the effect of date of heading was eliminated, suggesting that fruiting period and yield are positively correlated.

This suggestion is borne out by the correlations between yield and length of fruiting period, the values being $+0.337 \pm 0.060$ for the Pentad × Nodak strains, $+0.394 \pm 0.046$ for the Pentad × Akrona strains, and $+0.505 \pm 0.067$ for the Nodak × Akrona strains. These values are greater than the partial coefficients mentioned above. Holding rust constant did not significantly change the relation between yield and fruiting period.

The coefficients for yield and gasoline color value and for yield and crude protein in most cases were not significant and in all cases were not important.

TEST WEIGHT AND OTHER CHARACTERS

The relations of test weight to yield and rust have been discussed. In only one of the crosses, namely, Pentad × Akrona, were the data such as to permit the calculation of the correlation coefficients for test weight and plumpness. This value is $+0.627 \pm 0.048$. Holding rust constant reduced the value somewhat, but holding constant the length of fruiting period had no effect.

The coefficient for test weight and weight of kernels was not significant in the Pentad × Nodak cross, but in the Pentad × Akrona cross the value is $+0.468 \pm 0.062$, which was only partly lessened by eliminating the effects of rust and length of the fruiting period.

Test weight gave indications of being related to heading, ripening, and length of fruiting period in the same manner as was yield, but lack of parental differences in test weight in the Pentad × Nodak cross, and lack of any test-weight data on the Nodak × Akrona cross prevents the drawing of a clearer picture of these relations. In the Pentad × Akrona hybrids, test weight was correlated with heading date to the extent of -0.251 ± 0.074 and with ripening date to the extent of $+0.226 \pm 0.075$. Each of these values was increased by holding constant ripening date and heading date, respectively, but not enough to equal the coefficient for test weight and length of fruiting period, which is $+0.388 \pm 0.067$. This latter relation held with the effect of rust eliminated.

Test weight was not significantly related to gasoline color value nor to protein.

PLUMPNESS AND OTHER CHARACTERS

The correlation coefficient between plumpness of kernel and weight per 1,000 kernels was high, the simple coefficients being $+0.635 \pm 0.034$ for Pentad × Akrona and $+0.756 \pm 0.034$ for Nodak × Akrona. It may be concluded that the estimates of plumpness were fairly accurate, since a perfect correlation between plumpness and kernel weight would not be expected because some portion of the variability in kernel weight must be attributed to variations in size and shape of kernel. This is especially true in the Pentad × Akrona cross in which the parents differ markedly in these respects.

The relation of plumpness to dates of heading and ripening and to length of fruiting period is not definite, and plumpness of kernel was not significantly correlated with gasoline color value or protein content.

WEIGHT OF KERNELS AND OTHER CHARACTERS

There appears to be a tendency for the early-heading strains to be higher in kernel weight, as determined by weight per 1,000 kernels.

No significant values were obtained for the relation between weight of kernel and date of ripening, but the coefficients for kernel weight and fruiting period were $+0.275 \pm 0.063$ for the Pentad × Nodak cross and $+0.378 \pm 0.049$ for the Pentad × Akrona cross.

The apparently inconsistent values for the correlation between kernel weight and protein may be explained by differences in the rust susceptibility of the hybrids. Thus, in the Pentad × Nodak cross, in which rust is but an insignificant factor in kernel weight, the negative correlation of -0.236 ± 0.064 indicates the usual condition—that when rust is not the main factor the lighter grain generally contains a higher percentage of protein. The partial coefficient holding constant rust infection raised the value to -0.288 ± 0.062. In the other two crosses rust is a more important factor, however, and since it lowers both kernel weight and percentage of protein, these characters tend to be positively correlated. The coefficient for the Pentad × Akrona strains was $+0.184 \pm 0.055$ and for the Nodak × Akrona strains, $+0.175 \pm 0.078$, the latter not being significant. These values were reduced almost to zero by holding constant the rust reaction.

No correlation was found between kernel weight and gasoline color value in any of the three crosses.

DATE OF HEADING AND OTHER CHARACTERS

A consistent positive correlation was found to exist between date of heading and date of ripening. This is in line with field observations that the wheats which head early tend also to ripen early.

Pentad × Nodak was the only one of the three crosses that showed a correlation between date of heading and gasoline color value, and this is barely significant.

The relation of date of heading to protein content also was not clear from the different significant correlations, which were -0.238 ± 0.052 for Pentad × Akrona and $+0.229 \pm 0.065$ for Nodak × Akrona.

DATE OF RIPENING, GASOLINE COLOR VALUE, AND PROTEIN CONTENT

There appears to be some tendency for the earlier ripening strains of the Pentad × Akrona cross to be higher both in gasoline color value and in protein content, but this was not true for the Nodak ×

Akrona cross, any relation that exists possibly being obscured by the tendency of the very rusty strains of this cross to dry up and ripen prematurely.

FRUITING PERIOD, GASOLINE COLOR VALUE, AND PROTEIN CONTENT

The negative coefficients for fruiting period and gasoline color value suggest a tendency for durum wheats with a short fruiting period to be higher in gasoline color value than those with a longer fruiting period, although the coefficients in all cases are small and in one case not significant. This bears out previous observations that the carotin content is higher in wheat that matures quickly in a hot, dry season than in wheat that ripens more slowly because of cooler temperatures.

The relation between fruiting period and protein content was not definite. Only the Nodak × Akrona cross gave a significant negative value, -0.272 ± 0.064. As might be expected, the value of the coefficient was increased somewhat by holding constant the effect of rust.

GASOLINE COLOR VALUE AND PROTEIN CONTENT

As both gasoline color value and protein content are the results of many and diverse factors, there may be no marked or consistent relation between them. Only in the Nodak × Akrona strains the correlation, -0.261 ± 0.064, is significant and shows a tendency for the strains low in gasoline color value to be higher in protein content. Such a correlation does not necessarily indicate any definite relationship between the two characters but, rather, is suggestive of contrasting responses to any common causal factors.

SUMMARY

Segregation of, and associations among, the characters of stem-rust reaction, yield per plant, test weight per bushel, kernel plumpness, kernel weight, date of heading, date of ripening, length of fruiting period, gasoline color value, and crude-protein content were studied in the three crosses involving Pentad, Nodak, and Akrona durum wheats.

Data on stem-rust reaction were taken in both F_2 and F_3, but for the other characters the results from the F_3 strains only were used. The parents exhibited three degrees of rust reaction—Pentad was strongly resistant, Nodak was weakly resistant, and Akrona was susceptible. Major consideration was given to the inheritance of rust reaction and its relation to other characters.

In all three crosses reaction to stem rust was inherited in a quantitative manner. No rust-free or immune plants were obtained. The different degrees of resistance of the Pentad and Nodak parents were inherited as recessive characters. Susceptibility was incompletely or only partly dominant over resistance. The average infection and proportion of heterozygous strains, as measured by the standard deviations for rust infection of each F_3 strain from the Pentad × Akrona cross, indicated that the resistant and susceptible parents differed in at least two major genetic factors. In the Pentad × Nodak cross the parents appeared to differ by two complementary minor factors differing in amount of effect. The Nodak × Akrona cross showed the most complicated inheritance, although two major factor differences are strongly indicated. There was a tendency toward transgressive segregation in the direction of susceptibility in

both the Pentad × Nodak and the Nodak × Akrona crosses. This, together with the difficulty of recovering the resistance of the Nodak parent and of the few homozygous intermediate strains, also suggested the presence of the two minor factors of the Pentad × Nodak cross or additional modifying factors in the Nodak × Akrona cross. The F_2 plant reaction was a fairly reliable indication of breeding behavior in F_3, and selected F_3 strains of Pentad × Akrona tested in F_4 proved homozygous for degrees of infection intermediate between the parents.

The segregation of the other characters was indicated by averages and standard deviations of the row-mean distributions. In most cases the character means of the hybrids were intermediate between those of the parents. Occasionally a hybrid exceeded one or both parents, but it was not determined whether this was owing to transgressive segregations or to other causes. The range of the hybrid averages of yield, test weight, and plumpness and weight of kernel tended to widen when stem rust was an important factor in the variability. Although their manner of inheritance appeared complex and their expression was influenced by environment, it seems reasonable to conclude that all the characters considered in this study are fundamentally hereditary and are transmitted in the same manner as are botanical characters.

The associations among the characters were studied by means of simple and partial correlation coefficients. The correlation between the reaction to stem rust of F_2 plants and the behavior of their progenies in F_3 was consistently significant and positive. Negative correlation coefficients demonstrated that rust reduced the yield, test weight, plumpness and weight of kernel, and crude-protein content.

Partial correlations showed that the positive correlation between yield per plant and test weight per strain is caused largely by the reduction of both characters by stem rust.

Partial correlations also indicated that the high correlation between yield and kernel plumpness was rather independent of fluctuations in rust or in length of fruiting period. The positive correlation between yield per plant and weight of kernel was considerably affected by the common relation of these characters to stem rust. Yield was favored by early heading and late ripening, that is, a long fruiting period, and these relations were little affected by variations in stem rust.

The relation of plumpness and weight of kernel to test weight was moderately close and only partly caused by variations in rust and in length of fruiting period. As in the case of yield, the strains that headed earlier and ripened later, or that had longer fruiting periods tended to show higher test weight.

Plumpness was closely correlated with kernel weight. Both kernel plumpness and kernel weight tended to show the same relations to heading and ripening dates and length of fruiting period as did yield and test weight.

There was a consistent positive correlation between heading and ripening dates. This masked the true relation of either to such characters as yield and test weight, which were related negatively to heading but positively to ripening. Shorter fruiting period tended to favor higher gasoline color values.

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