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Correlated Inheritance in Oats of Reaction to Diseases and Other Characters

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DAVID CLYDE SMITH[2]

INTRODUCTION

Stem and crown rust, caused by *Puccinia graminis avenae* Erikss. and Henn. and *Puccinia coronata* Corda, respectively, are two of the most destructive diseases of oats in the United States. They are widespread, and, tho often occurring in local areas only, may exist as general epiphytotics.

These two diseases are caused by fungi, each consisting of many specialized races or forms and each characterized by having different parasitic capabilities on the same varieties of oats. These differences in varietal reaction have been proved to be due to genetic factors. A variety may be resistant to all, several, or none of the known races of the organism.

The possibility of combining, by hybridization, the factors for resistance from two or more varieties into one improved strain makes the knowledge of the interrelationships of these factors, and the presence of favorable or unfavorable linkages in hybrid progenies, of cardinal importance to the breeder of disease-resistant strains.

Combination of resistance to diseases with desirable agronomic characters has been an important phase of the Minnesota Agricultural Experiment Station's oat-improvement program for many years. Varieties resistant to prevalent physiologic forms of stem rust have been obtained by hybridization and are now being grown extensively in the state. Using similar methods, smut resistance has been added to rust resistance in highly desirable agronomic strains. At the present time breeding work to incorporate resistance to crown rust with resistance to stem rust and smut is in progress.

Inheritance of resistance to stem rust of oats has been studied by several investigators. The manner of inheritance of crown-rust reaction is less well understood. The objects of the experiments reported herein were to study further the method of inheritance of stem-rust and

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crown-rust reaction and to investigate possible associations of stem-rust reaction with other characters. Straw characters have been studied in relation to inheritance of straw strength.

REVIEW OF LITERATURE

Stem-Rust Investigations

Varietal resistance.—Many workers have reported the results of observations on varietal reaction of oats to stem rust. Parker (26), in 1918, described White Tartar and Ruakura Rustproof as resistant varieties. Durrell and Parker (10), 1920, reported Green Russian, White Tartar, and Ruakura Rustproof to be the most resistant of several oat strains tested. A similarity of reaction was noted between greenhouse tests of seedlings and field tests of older plants, tho considerable variation existed in the amount of rust on plants in the field. Greenhouse results were considered to affirm field reaction. Mackie and Allen (22), in 1924, reported the results of stem-rust observations on 217 oat varieties. Of these, Richland, Green Russian, Ruakura, White Russian, and Snoma showed marked resistance. Levine, Stakman, and Stanton (21), 1930, concluded that Iogold, Hajira, Richland, (Minota x White Russian), White Russian, Green Mountain, Anthony, and Edkin were the most resistant of numerous varieties grown at many stations in the United States over a five-year period. Other workers have made essentially similar observations regarding varietal reaction to stem rust.

Physiologic specialization.—Stakman, Levine, and Bailey (30), in 1923, first reported the existence of physiologic forms in the stem-rust organism *Puccinia graminis avenae*. Four such forms were determined on the basis of differential host reactions, and the presence of a fifth form was indicated. Bailey (1), in 1925, reported the isolation of five physiologic forms from stem-rust collections made in the United States.

Gordon (15) made known the results of a survey of Canadian forms in 1928. Forms 2 and 5 were found to predominate. The existence of a virulent form, No. 6, was also discovered. In 1928, Gordon and Bailey (16) observed six physiologic forms in Canada. Gordon and Welsh (17), in 1932, reported results of more extensive studies. From 1,257 collections of stem rust made in Canada, nine physiologic forms were isolated. Of these, Forms 1, 2, and 5 were most prevalent. A tenth form is now known. Forms 2 and 5 are most common, and all known physiologic forms have not been collected in the United States.

Inheritance.—The nature of the inheritance of reaction to *Puccinia graminis avenae* has been studied by several investigators.

In 1921, Garber (13) published preliminary results which indicated that resistance to stem rust was dominant and that segregation occurred on a single-factor pair basis. In 1922 (14) a second paper confirmed the earlier conclusions. The crosses studied were Minota and Victory (susceptible) x White Russian (resistant). Griffee (18), 1922, obtained further evidence supporting the single-factor pair explanation for differentiation of stem-rust reaction and called attention to the possibility of eliminating heterozygous resistant plant selections by testing seedling progenies from selected plants in the greenhouse.

Hayes, Griffee, Stevenson, and Lunden (19), 1928, in crosses of rust-resistant selections of Minota or Victory x White Russian with Black Mesdag (susceptible) found the resistant type to be dominant on a single-factor basis. Dietz (7), 1925, and (8), 1928, found a similar explanation of inheritance satisfactory in crosses of White Russian with National and Lincoln, two susceptible varieties. In the Burt variety three genetically different, susceptible strains were found. One of these, when crossed with White Russian, gave ratios of three resistant to 13 susceptible in F_2. Progenies from the resistant F_2 plants segregated in F_3 into three resistant to one susceptible. Another Burt strain used in crosses with White Russian gave an F_2 ratio of three resistant to one susceptible, while the progeny from crosses using a third Burt strain gave an F_2 ratio of one resistant to three susceptible. Crosses between Green Russian and Ruakura, both resistant varieties, produced resistant F_1 plants and some F_2 plants more resistant than either parent. This was the case also in crosses between White Russian and Ruakura, both resistant varieties.

Waterhouse, cited by Welsh (35), first studied the reaction of F_2 progenies to a single known physiologic form, tho it is possible that previous workers may have had similar conditions. F_2 progenies of the crosses Belar x Reid and Ruakura x Richland were observed to segregate for reaction on a single-factor basis where Physiologic Form 1 only was present. Resistance was dominant in the F_1 generations.

Welsh (35), 1931, studied the reactions of hybrid progenies from crosses of varieties tested for reaction to eight different forms of *P. g. avenae*. The results of varietal tests agree with those already given. (Table 1). Monarch was found to belong in the same reaction class as Richland. A test of a (Minota x White Russian) x Black Mesdag selection gave results similar to those for White Russian. The reactions of Markton and Banner were similar to that of Victory. Observations on hybrid progenies were made in both field and greenhouse. An artificial field epiphytotic was developed, using Physiologic Forms 1, 2, 3, 5, and 7. In crosses of Heigira Strain x Banner resistance to Forms 1, 2, 3, 5, and 7 appeared to be controlled by a single-factor pair. In crosses of Markton x Heigira Strain and Victory x Green Russian,

resistance proved to be dominant and segregation to occur on a one-factor pair basis. Similar results were obtained in crosses of Heigira Strain x Joanette. In the latter cross, data obtained from testing F_3 seedling reactions from random F_2 plants to Form 4 suggested a 9:7 ratio tho the evidence was not considered conclusive. In crosses of Joanette Strain with (Minota x White Russian) x Black Mesdag, resistance to Form 4 was dominant and conditioned by a single-factor pair. Similar results were obtained with progenies of Richland with (Minota x White Russian) x Black Mesdag.

Gordon and Welsh (17), 1932, found resistance to Form 4 to be inherited independently of resistance to Forms 1, 2, 3, 5, and 7 and to depend on a single factor, in a Heigira Strain x Joanette cross. Resistance to Form 4 was also observed to be dominant in a cross between Joanette and (Minota x White Russian) x Black Mesdag. In five other crosses between resistant and susceptible varieties, resistance was found to be dominant and determined by a single factor. Inheritance of reaction to stem rust of adult plants in the field was concluded to be determined by the same factors as controlled seedling reaction in the greenhouse.

Several investigators have observed the nature of associations of rust reaction with other plant characters. Garber (14), 1922, observed rust reaction to be independent of panicle type. Hayes, Griffee, Stevenson, and Lunden (19), 1928, found no association between rust reaction and lemma color, awn development, or smut reaction. Welsh (35), 1931, reported rust reaction not to be associated with lemma color or maturity.

Straw Strength

Welton and Morris (36), 1931, reported studies of a number of factors related to lodging of oats. Stiff-strawed varieties were designated as having larger culm diameters and consequently higher breaking strength. Davis and Stanton (6), 1932, presented the results of straw-breaking tests of many oat varieties. A correlation coefficient of $.863 \pm .030$ was obtained for breaking strength between 1929 and 1930 data, based on 32 varieties of oats. In general, stiff-strawed varieties were found to show highest resistance to breaking. Clark and Wilson (3), 1933, described an apparatus used in measuring breaking strength in straw of small grains and gave results of breaking tests. While differences in breaking strength were significant among varieties of wheat, there was no correlation between breaking strength and lodging in two series of data studied.

Crown-Rust Investigations

Varietal resistance.—Parker (26), in 1918, reported Burt, Cook, Appler, Italian Rustproof, Ruakura Rustproof, and Turkish Rustproof

oats to be very resistant to crown rust. Durrell and Parker (10), 1920, found varieties of the red oat group to be more resistant to crown rust than those from the common oat group. Of the former, Appler, Burt, Early Ripe, and Golden Rustproof showed greatest resistance. Levine, Stakman, and Stanton (21), 1930, observed Green Mountain, Red Rustproof, Iowar, "Rustless" Selection, Burt, and Ruakura to be most resistant to crown rust in extensive field studies in the United States.

Murphy (24) observed varieties resistant as seedlings to be resistant in the field, no varieties being more susceptible as adult plants than as seedlings. Varieties susceptible as seedlings were not always susceptible as adults.

Physiologic specialization.—Physiologic specialization in *Puccinia coronata* was first demonstrated in this country by Hoerner (20) in 1919. Four physiologic forms were distinguished, based on the reactions of Green Russian and Ruakura Rustproof. Popp (29), 1926, recognized four physiologic forms in studying 22 crown-rust cultures from five provinces of eastern Canada. Parson (29), 1927, was able to distinguish five physiologic forms of *P. coronata,* using four differential varieties.

Murphy (23), 1930, isolated nine physiologic forms of *P. coronata* from single uredospore isolations from 45 collections on *Avenae* and *Rhamnus* species. Eight of 33 oat varieties tested could be used as differential hosts.

Murphy (24), 1934, using 11 differential hosts, distinguished 32 physiologic forms from rust collections made in the United States. Certain forms appeared to be confined to local areas, while others were more general in occurrence. In the southern states Forms 1, 3, and 7 were most common, but these forms were seldom collected in the northern states. Forms 2, 6 and others appeared to be northern forms, while Form 24 and certain others were wide-spread. Form 1 was considered to be extremely virulent.

Frenzel (12), 1930, studied 55 cultures from 27 collections of *P. coronata* made in Germany and recognized 33 forms based on the differential reactions of nine varieties. On the basis of present knowledge, more physiologic forms appear to exist in *P. coronata* than in *P. graminis avenae.*

Inheritance.—Parker (27), 1920, studied crown-rust reaction in a cross of Burt (resistant) x 60 Day (susceptible). The reaction of the F_1 plants was not observed. In the F_2 generation 468 inoculated seedlings were classified as 81 resistant, 61 intermediate, and 326 susceptible. It was concluded that susceptibility was partially dominant and that multiple factors controlled the reaction. Adult plants were reported to act similar to seedlings. Davies and Jones (4), 1926, in a cross between resistant Red Rustproof and susceptible Scotch Potato

oats, reported resistance to be partially dominant in the F_1 plants. The F_2 generation segregated as three resistant to one susceptible. The classification into resistant and susceptible types was described as being unquestionable, tho within the resistant group slight variations ranging from weakly developed sori to complete absence of rust were noted. Most resistant seedlings were in the latter class. Data on F_3 seedlings (5) seemed to substantiate the F_2 classification. There was slight indication that heterozygous resistant seedlings formed weakly developed uredo-sori, while homozygous resistant seedlings showed not even slight infection. Incomplete dominance, or the presence of some modifying factor, was suggested as an explanation. Dietz and Murphy (9), 1930, in studies of F_1, F_2, and F_3 generations of crosses between resistant and susceptible varieties found susceptibility dominant and reaction to be determined by two-factor pairs, one of which acted as an inhibitor of resistance. In a cross between Sunrise (resistant) x Fulghum (susceptible) the F_1 was susceptible and the F_2 segregated in the ratio of 13 susceptible to three resistant. F_3 data supported the hypothesis that the genotype of the resistant parent might be designated as SSii and that of the susceptible parent as ssII.

EXPERIMENTAL METHODS AND MATERIALS

Stem-Rust Studies

A description of the methods and materials used will be given separately for each of the three phases of the studies. The varieties used as parents of the progenies studied in these experiments were Gopher and Rainbow. Gopher has been described by Stanton, Griffee, and Etheridge (32), and Rainbow has been described by Stanton, Gaines, and Love (31). Wilson and Arny (37) have described both Gopher and Rainbow.

Gopher is a pure line selection from 60-Day made at the Minnesota Agricultural Experiment Station. Rainbow is a pure line selection from Green Russian obtained by the North Dakota Agricultural Experiment Station.

The important contrasted characters of the Gopher and Rainbow varieties are listed as follows:

Gopher	Rainbow
Early season	Mid-season
Strong-strawed	Weak-strawed
White lemma	Yellow lemma
Susceptible to stem rust	Resistant to stem rust
Basal hairs on grain	Basal hairs absent

Tho susceptible to stem rust, Gopher, because of earliness, often escapes infection under field conditions.

Using the nomenclature of Stakman, Levine, and Bailey (30), the descriptions for the types of stem-rust reaction of seedlings encountered in the present studies are as follows:

Class 1. "Extremely resistant. Infection very light; uredinia minute and scattered and surrounded by very sharply defined necrotic areas." This is the Rainbow type of reaction to Forms 1, 2, 3, 5, and 7 and is shown in Plate 1, Figure 1 at C.

Class 2. "Moderately resistant. Infection light; uredinia usually small and scattered; hypersensitive, varying from sharply defined necrosis to pronounced chlorosis." This is the White Tartar reaction to Forms 1, 2, 5, 8, and 9 of stem rust and is identical with the "3±" of Griffee (18). This reaction is shown in Plate 1, Figure 1 at A. Because of the large numbers of pustules, hypersensitive areas are not prominent.

Class 4. "Completely susceptible. Infection normal and heavy; uredinia large, numerous and confluent; hypersenitiveness entirely absent but chlorosis may be present when cultural conditions are unfavorable." (Plate I, Figure 3.)

Class X. Heterogeneous reaction. The reaction designated as x is based on a mixture of pustule types such that "susceptible" and "resistant" reactions occur on the same seedling leaf even tho only one physiologic form of rust is present. Reactions of this type are illustrated in Plate 1, Figure 4, as the two central panels of B and C.

The crosses were made between individual plants of the Gopher and Rainbow parents, and it was possible to compare the results of studies of crosses with those of the actual parents used. As will be noted later, the Gopher parent used differed in stem-rust reaction from that obtained with the standard Gopher variety.

The F_1 generation, consisting of four plants on whose progenies detailed studies were made later, was grown in the field in 1931 and no data were obtained. The F_2 generations from these and other F_1's of the same cross were grown under an artificial stem-rust epiphytotic caused by Forms 2, 3, 5, and 7. These forms were increased on border rows of Victory by transplanting infected greenhouse plants and by use of the hypodermic method of inoculating growing plants in the border rows. Plantings of the parent varieties served for use as checks. F_2 plants and parents were classified for rust reaction, and 432 F_2 plants taken at random were studied in detail for awn character, color of lemma, and basal hairs. Plants were classified for rust reaction as resistant, intermediate, and susceptible. Awns were measured for

length in millimeters and classified as strong, medium, or weak, according to the development of the geniculate character. Plants were also classified for awn presence as awnless, weak, medium, and strong, and for lemma color as yellow or white. Four classes were made for the development of basal hairs.

One hundred ninety-nine F_3 seedling families, taken at random from the 432 F_2 plants previously referred to, were tested individually in the greenhouse for reactions to each of the physiologic forms, Nos. 1 to 9, of *Puccinia graminis avenae*. Families consisting of about 40 plants from each of the 432 F_2 plants were subjected to a field epiphytotic of stem rust in 1933. Parental and progeny reactions are shown in Plate II. These families were classified in the field for stem-rust reaction. Ninety-eight F_3 families were studied in similar detail as the 432 plants of the F_2 generation.

Plant families of 276 F_2 plants selected for resistance in the field rust nursery in 1932 were tested in the greenhouse for seedling reaction to Forms 1, 2, 3, 5, and 7. F_3 families of these selections were also grown in the rust nursery in 1933 and classified for rust reaction. From F_2 material not in the rust nursery but near to it, enough rust developed to permit selection of 162 F_2 plants of known field resistance for which were determined F_3 seedling reactions to the five forms of rust previously indicated. F_3 progenies were grown also in the rust nursery in 1933 and classified for rust reaction. In all plantings parents occurred every ten rows.

An F_2 progeny, and parents, of another Gopher x Rainbow cross were grown in the stem-rust nursery in 1933. This progeny was studied in detail.

Straw Strength

From the nursery not under the rust epiphytotic but near to it, 467 F_2 plants were taken at random in 1932. These plants were studied for culm diameter and breaking strength. Data were taken on the parents and hybrids, and a study was made of the correlation between the breaking strength of F_2 plants and the means of their F_3 progenies.

The diameter of the main culm at the center of the second internode above ground was measured to the nearest .05 millimeter, and the breaking strength in grams at this point determined using the device manufactured by Paul Polikeit, Halle A. S., Germany, and described by Clark and Wilson (3).

Crown-Rust Studies

The varieties used in crown-rust studies were Victoria, Anthony, Minrus, Iogold, Rainbow, and Double Cross II-22-220.

Victoria is a variety belonging to the *Avena sativa* group. It is highly resistant to all known physiologic forms of crown rust and has

been described in detail by Murphy and Stanton (25) and Stanton and Murphy (34). Little is known of the varietal reactions of these oat strains to individual forms. Anthony has been described by Stanton, Gaines, and Love (31). A description of Iogold has been published by Stanton, Love, and Gaines (33) and also by Burnett (2). Minrus has been described by Wilson and Arny (37) as Minn. 693. These writers have also described Anthony, Iogold, and Rainbow. Double Cross II-22-220 is a high-yielding, smut-resistant Minnesota strain, obtained from (Minota x White Russian) x Black Mesdag and possesses the stem-rust resistance of White Russian. It is quite susceptible to crown rust.

Greenhouse tests of seedlings were made using technic similar to that employed in the stem-rust studies.

Differentiation of types of reaction to crown rust required a rather extensive code. Six classes were made. These were:

Class 0. Pustules minute or absent, leaves showing very small necrotic areas. Leaf tips often necrotic. Leaves not atrophied. Plate III, Figure 1A, central panel.

Class 1. Pustules small, necrotic areas better defined than in Class 0. No, or slight, atrophy. Plate III, Figure 1B, left panel.

Class 2. Pustules small, more frequent. Leaves heavily necrosed, showing slight to extreme atrophy. Plate III, Figure 1C or 1D, left panel.

Class 3. Pustules somewhat larger and more numerous. General necrosis of heavily infected areas. Atrophy usually extreme. Plate III, Figure 1C or 1D, central panel, or Figure 2B, two right panels.

Class 4. Pustules large. Necrosis absent. Chlorosis may be present. Plate III, Figure 1C or 1D, right panel.

Class X. Large infrequent pustules intermingled with light necrotic areas having no or small pustules. Plate III, Figure 1A, left panel, or 1B, right panel.

In some cases reaction types were also designated as + or — when uncertainty as to class was encountered. The reaction designated as x may have been due to mixed physiologic forms.

In 1933 considerable hybrid and parental material was grown in a crown-rust nursery in the field. Border rows were planted of several susceptible varieties which at the early booting stage were inoculated with uredospore suspensions with the use of a hypodermic needle. Crown Rust Forms 1, 2, 3, 4, 6, 7, 17, and 24 were used as inoculum in the field studies. A medium heavy epiphytotic of crown rust developed, and except for one small dry area it was quite uniform in the nursery.

Six classes for crown-rust reaction were made in the field, and plants were tagged with class numbers before maturity. The types of rust reaction set up for the field classification are shown in Plate IV, Figure 3. Classes 1, 2, and 3 were those showing some degree of necrosis and increasing amounts of rust with higher numbers. Classes 4, 5, and 6 were made for plants showing little or no rust necrosis and for increasing frequency and size of pustules. Plants which showed no necrosis or pustules in the field were labelled as mature and were not included in the summaries of rust reaction.

EXPERIMENTAL RESULTS

Stem-Rust Studies

At present oat varieties may be divided into four general groups as to reaction in the seedling stage to the nine better known forms of *Puccinia graminis avenae*. These groups and a few of the varieties occuring in each are shown in Table 1.

Table 1

Several Common Oat Varieties Grouped According to Mode of Seedling Reaction to Nine Physiologic Forms of *Puccinia graminis avenae*

	Variety	Type of reaction to Physiologic Forms								
		1	2	3	4	5	6	7	8	9
Group I	Rainbow	1	1	1	4	1	4	1	4	x
	Iogold	1	1	1	4	1	4	1	4	x
	Richland	1	1	1	4	1	4	1	4	x
	Hajira	1	1	1	4	1	4	1	4	x
Group II	White Russian	2	2	4	4	2	4	4	2	2
	Green Mountain	2	2	4	4	2	4	4	2	2
	Anthony	2	2	4	4	2	4	4	2	2
	Minrus	2	2	4	4	2	4	4	2	2
Group III	Joanette	1	4	1	1	x	4	4	4	4
Group IV	Gopher	4	4	4	4	4	4	4	4	4
	Victory	4	4	4	4	4	4	4	4	4
	Swedish Select	4	4	4	4	4	4	4	4	4

As may be noted in Table 1, the resistance of the first group of varieties to Physiologic Forms 1, 2, and 5 is a little more pronounced than that of the second group. Except for Form 6, varietal resistance to all forms of *Puccinia graminis avenae* is known to occur. From a study of Table 1, it will be noted that typical Gopher is susceptible in the seedling stage to all forms. The actual Gopher parent used in the Gopher x Rainbow crosses of these experiments answered the varietal description previously given, with the important difference that the stem-rust reaction was similar to that of the White Russian variety, the strain being moderately resistant to Forms 1, 2, 5, and 9 and susceptible

to Forms 3, 4, 6, 7, and 8. White Russian is, however, moderately resistant to Form 8. The origin of this particular reaction in the Gopher Variety is unknown.

Table 2

Goodness-of-Fit Tests to a 3:1 Ratio of 20 F_2 Progenies of Gopher x Rainbow

	O	C	O-C	$(O-C)^2$	$(O-C)^2/C$
R*	70	63	7	49	.7778
S*	14	21	7	49	2.3333
R	14	15	1	1	.6667
S	6	5	1	1	.2000
R	69	71	2	4	.0563
S	26	24	2	4	.1667
R	57	58	1	1	.0172
S	20	19	1	1	.0526
R	70	67	3	9	.1343
S	19	22	3	9	.4091
R	15	14	1	1	.0714
S	3	4	1	1	.2500
R	46	43	3	9	.2093
S	11	14	3	9	.6429
R	22	22	0		
S	7	7	0		
R	84	82	2	4	.0488
S	25	27	2	4	.1481
R	64	61	3	9	.1475
S	17	20	3	9	.4500
R	49	45	4	16	.3556
S	11	15	4	16	1.0667
R	12	12	0		
S	4	4	0		
R	74	76	2	4	.0526
S	27	25	2	4	.1600
R	83	84	1	1	.0119
S	29	28	1	1	.0357
R	86	86	0		
S	28	28	0		
R	123	119	4	16	.1345
S	36	40	4	16	.4000
R	67	65	2	4	.0615
S	20	22	2	4	.1818
R	83	83	0		
S	27	27	0		
R	76	77	1	1	.0130
S	27	26	1	1	.0385
R	51	53	2	4	.0755
S	19	17	2	4	.2363
	1593				$X^2 = 9.6056$

* R—resistant.
S—susceptible.

Field-rust reaction.—Twenty F_2 progenies totalling 1,593 plants were classified as resistant, intermediate, susceptible, and dead in the stem-rust nursery in 1932. Dead plants were considered to be those prematurely ripe and of uncertain rust reaction. Grouping resistant and intermediate classes together as resistant and eliminating those prematurely ripe gives a close approach to a ratio of three resistant to one susceptible, as indicated in Table 2.

Table 3

Breeding Behavior of F_3 Families of Gopher x Rainbow in Comparison with the F_2 Classification for Stem-Rust Reaction, with Figures in Per cent of the Total Population

F_2 Field Classes	F_3 Seedling reaction		
	Resistant	Segregating	Susceptible
Resistant	54.76	45.24	0.00
Intermediate	25.00	72.73	2.27
Susceptible	0.00	9.43	90.57
Dead	37.50	31.25	31.25

X^2 for the .05 point and 1 degree of freedom is 3.841. Hence no F_2 progeny fails to agree, within reasonable limits of variation, to a 3:1 ratio. The total X^2 for the 20 progenies reaches a value of 9.6056, which, for 20 degrees of freedom, corresponds to a P value of .98 to .95.

From the 1,593 F_2 plants, four complete F_2 progenies consisting of 432 plants were taken for a detailed study of other plant characters.

The accuracy of the field classification for rust reaction in F_2 was checked on the basis of reactions of F_3 seedlings from F_2 plants. The percentage relationships are shown in Table 3.

Table 4

Goodness-of-fit Tests to a 3:1 Ratio of F_2 Progenies Corrected on the Basis of F_3 Reaction

Progeny	O	C	O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
359 R*	80	79	1	1	.0127
S	25	26	1	1	.0385
360 R	108	108	0	0	
S	36	36	0	0	
361 R	55	60	5	25	.4167
S	25	20	5	25	1.2500
363 R	74	76	2	4	.0526
S	28	26	2	4	.1429
					$X^2 = 1.9134$

* R—resistant.
S—susceptible.

These data indicate the difficulty of classification into heterozygous (intermediate) and homozygous (resistant) groups and also the phenotypic variation in these classes. Premature ripening of plants appears to be independent of rust reaction in these tests.

On the basis of F_3 seedling reactions, the corrected F_2 ratios and goodness-of-fit for a 3:1 ratio for the four F_2 progenies taken for further study are shown in Table 4.

For an X^2 value of 1.9134 and 4 degrees of freedom, P for goodness-of-fit is between .80 and .70 and indicates a good agreement to a 3:1 ratio. These data may therefore be considered to demonstrate that the plants and progenies taken for further studies were at random in regard to rust reaction.

Contingency studies.—The 432 F_2 plants taken at random were classified for certain other characters. Table 5, Part 1, gives the results of X^2 tests for independence made on rust reaction and other characters.

Table 5

X^2 Tests for Independence of Rust Reaction and Other Characters in 432 F_2 Plants of a Gopher x Rainbow Cross

Characters	X^2 Values	Degrees of freedom	P
Part 1			
Rust reaction and breaking strength	14.4925	12	.20 to .30
" " " culm diameter	5.2162	12	.98 to .95
" " " lemma color	1.3566	2	.99 to .98
" " " basal hairs	2.4834	6	.90 to .80
" " " awn strength	13.8676	6	.05 to .02
" " " blast in F_3 families ..	6.8552	8	.70 to .50
Part 2			
Lemma color and awn presence	88.0701	3	Less than .01
" " " " strength	115.1000	3	" " "
" " " " length*	68.6733	7	" " "
" " " basal bristles	63.8905	3	" " "
Awn strength and basal bristles	88.8479	9	" " "

* Based on 266 awned plants.

The values of X^2 obtained were referred to Fisher's table of X^2 (11) for the values of P, using the appropriate degrees of freedom. (D.f. = [r-1] [c-1]) According to Fisher, if P falls below .02 there is a real question as to the validity of the hypothesis tested. In the relation of awn strength, and rust reaction with a P value from .05 to .02, there is some question as to the independence of these characters. In the other cases independence is clearly indicated.

Many workers have shown the interrelation of basal bristles on the grain, length and development of awns, and lemma color. Part 2 of Table 5 indicates a high degree of association of these characters in the

Gopher x Rainbow progeny, the awn complex being associated with white lemma color.

An F_2 progeny of 162 plants of Gopher x Rainbow grown in the stem-rust nursery in 1932 was classified and observed in similar detail as the 432 plants previously studied. The value of P for goodness-of-fit to a 3:1 ratio for rust reaction in this progeny was .20 to .10. The values of X^2 for independence of rust reaction and other characters are given in Table 6.

Table 6

X^2 Tests for Independence of Rust Reaction and Other Characters in 162 F_2 Plants of a Gopher x Rainbow Cross

Characters	X^2 Values	Degrees of freedom	P
Part 1			
Rust reaction and breaking strength	2.9597	5	.80 to .70
" " " culm diameter	3.3750	5	.70 to .50
" " " lemma color	3.3704	1	.10 to .05
" " " basal hairs	1.3851	2	.70 to .50
" " " awn strength	8.5445	6	.30 to .20
" " " " length*	5.8159	5	.50 to .30
" " " " presence	6.7939	3	.10 to .05
Part 2			
Lemma color and awn presence	13.2108	3	Less than .01
" " " " strength	16.9559	3	" " "
" " " " length*	18.5337	5	" " "
" " " basal bristles	10.2387	2	" " "
Awn strength and basal bristles	42.5465	6	" " "

* Based on 118 awned plants.

The data in Table 6 are in essential agreement with the previous data except that there is no evidence of an association between rust reaction and awn strength. The values of X^2 for the interrelation of color and the awn complex are lower than those shown in Table 5, but as before P exceeds the .01 point.

Studies of seedling reaction to individual forms.—The seedling reaction types of the Gopher and Rainbow strains used in these experiments are indicated in Table 7.

Table 7

Seedling Reactions of Progenies of Gopher and Rainbow Parents to Individual Physiologic Forms of *P. graminis avenae*

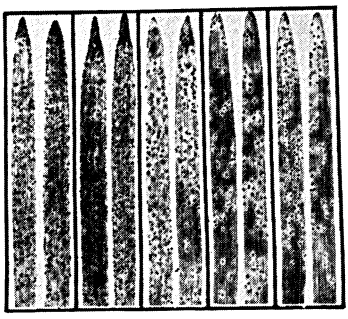
	Infection Types to Physiologic Forms								
	1	2	3	4	5	6	7	8	9
Gopher	2	2	4	4	2	4	4	4	2
Rainbow	1	1	1	4	1	4	1	4	x

In these experiments the reaction of Gopher is referred to as moderately resistant for Forms 1, 2, 5, and 9.

The reaction to Forms 1, 2, and 5 was a moderate resistance (Class 2) and designated "susceptible" only for comparison with Rainbow (Class 1). The segregates gave only Class 1 and Class 2 reactions as seedlings, when inoculated with Forms 1, 2, or 5. This type of segregation is shown in Plate 1, Figure 1. Segregation to Forms 3 and 7 also occurred with parental types only, or 1 and 4 reactions, appearing. This type of segregation is shown in Plate I, Figure 2. The 4 reaction is not well developed in the figure, because of numerous pustules and high greenhouse temperatures.

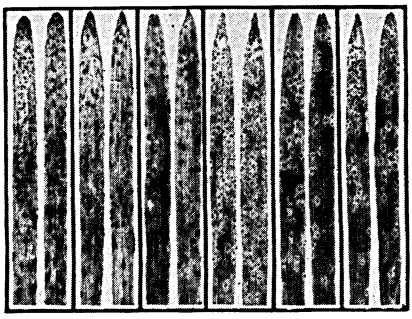
Both the Gopher and Rainbow parents were susceptible to Forms 4 and 6, no resistance being shown by plants of the parental strains or by the hybrids between them.

PLATE I



A B C

Figure 1

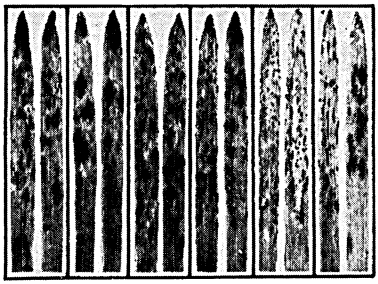


A B C

Figure 2

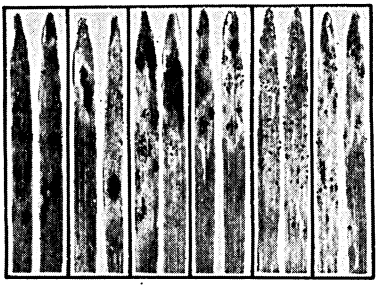
Fig. 1. Seedling reactions of Gopher (A), Progeny (B), and Rainbow (C) to Form 2 of *P.g. avenae*. Similar reactions were obtained to Forms 1 and 5.

Fig. 2. Seedling reactions of Gopher (A), Progeny (B), and Rainbow (C) to Form 3 of *P.g. avenae*. A similar reaction was obtained to Form 7.



A B C

Figure 3



A B C

Figure 4

Fig. 3. Seedling reactions of Gopher (A), Progeny (B), and Rainbow (C) to Form 4 of *P.g. avenae*. A similar reaction was obtained to Form 6.

Fig. 4. Seedling reactions of Gopher (A), Progeny (B), and Rainbow (C) to Form 9 of *P.g. avenae*.

(A and C represent one panel in each case. B represents progeny types, including all but one panel on each side.)

The reactions of the parents to Form 8 were susceptible, tho the pustule type on seedlings of the Gopher parent showed less development (Class 3) than when this parent was tested to other forms to which it was susceptible (Class 4).

F_3 progenies from the 432 plants classified for stem-rust reaction in F_2 were grown and tested individually in the seedling stage to Forms 1 to 9 of *Puccinia graminis avenae* in the greenhouse.

The agreement between the F_2 field classification and the F_3 seedling reaction was indicated in Table 3. The various reactions of seedlings of parents and progeny to the several physiologic forms are shown in Plate I.

The 199 families tested reacted in a similar manner to Physiologic Forms 1, 2, 3, 5, and 7. Families resistant to Form 1 were also resistant to Forms 2, 3, 5, and 7 and gave the characteristic Rainbow reaction to these forms. Families segregating for reaction to Form 1 segregated for reaction to Forms 2, 3, 5, and 7. Families susceptible to Form 1 were likewise susceptible to Forms 2, 3, 5, and 7, the typical Gopher reaction for each form being observed.

Similar agreement in reaction to Forms 1, 2, 3, 5, and 7 was observed in F_3 progenies from 432 plants selected as being resistant and intermediate in the F_2 generation. These progenies were tested separately also to Forms 1, 2, 3, 5, and 7.

The reactions of seedling progenies to Form 8 are difficult to explain. Families which bred true for resistance or susceptibility to Forms 1, 2, 3, 5, and 7, in earlier tests, bred true for susceptibility to Form 8. Families segregating for reaction to these forms segregated for reaction to Form 8, and no resistant seedling types were observed. Since no F_2 data were available on reaction to Form 8, it is more difficult to ascribe to any genetic regularity the results obtained for the segregating families. Action of complementary factors to produce a homozygous resistant type seems unlikely as no F_3 families were resistant. The possibility that resistance to Form 8 is a heterozygous character seems unlikely since summing of the segregates for the rust types obtained in 83 segregating F_3 families gives numbers of 570 resistant to 967 susceptible, which does not approximate the expected 2:2 ratio. Resistant individuals obtained in the segregating progenies were classified as Class 2 and Class 1. That such results are due to a mixture of forms appears unlikely since none of the susceptible families showed such types, tho part of these contained the allelomorphs conditioning resistance to other forms of rust. Parental reactions did indicate a slight mixture of Form 3 or 7.

The Gopher parent was moderately resistant to Form 9 as well as to Forms 1, 2, and 5. The Rainbow parent gave a mesothetic (x)

reaction to this form in most cases. Some Rainbow seedlings were also noted as showing Class 4 reaction. The F_3 seedling progenies within each of the three classes produced by growing resistant, segregating, or susceptible F_2 plants, respectively, gave similar reactions to Forms 1, 2, 3, 5, and 7. Seedlings were classified mainly as Class 2, and the x reaction was a combination of Class 2 and Class 4 pustules. During the period these progenies were grown, temperatures in the greenhouse were as high as 85° F., which is approximately 10 degrees higher than the temperatures at which other tests were carried on. Progenies from families susceptible to Forms 1, 2, 3, 5, and 7 appeared to breed more nearly true in reaction than those originating from resistant or heterozygous F_2 plants.

The reaction classes obtained in tests using Physiologic Form 9 are shown in Plate I, Figure 4. Tho most seedlings showed parental types, there were many of Class 4 reaction. Whether such individuals were genetically different from those classified as Class X is uncertain. The difficulty of recognizing the x reaction of Rainbow segregating out in the progeny, and the failure to separate it distinctly from other rust-reaction classes, renders the making of a definite conclusion with respect to the inheritance of reaction to this form impossible.

With the exception of two progenies, the 199 F_3 families tested in the greenhouse to individual forms of stem rust gave similar reactions when subjected to a field epidemic of Forms 1, 2, 3, 5, and 7. Families breeding true for resistance to these individual forms in the greenhouse also proved resistant to these forms in a mixed epiphytotic in the field. One family classified as resistant on the basis of greenhouse reaction was recorded as segregating in the field. One family classified as segregating in the greenhouse studies was described as resistant in the field. These two exceptions are considered to be due to error.

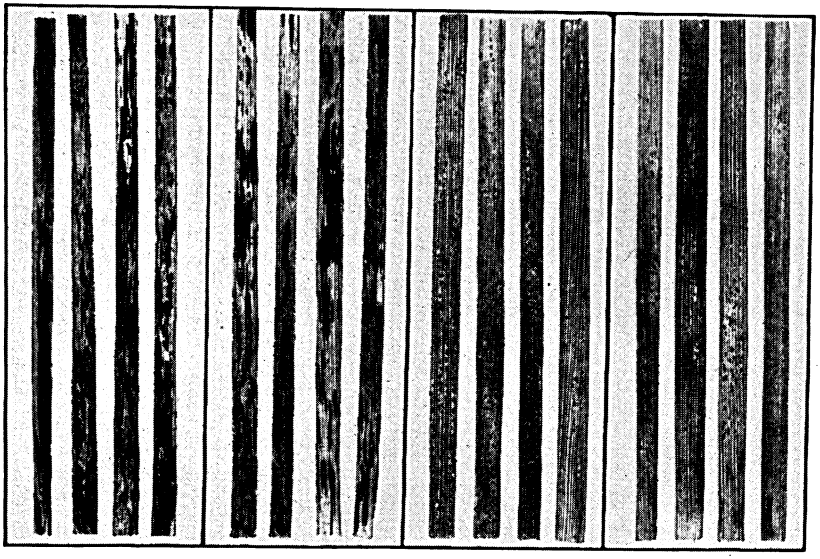
The F_3 families selected on the basis of resistance to stem rust in the seedling stage proved to be resistant in the field to a mixed epiphytotic of the fungus. The families segregating in the greenhouse segregated in the field.

Parent and progeny stem reactions to the rust organism are indicated in Plate II.

The presence of the different physiologic forms in the stem-rust nursery was checked in 1933. Twenty collections of rust uredospores were made in different parts of the nursery and each used to inoculate differential hosts. Form 7 was most prevalent and was identified nine times. Form 3 was isolated three times; Form 2, five times; Form 5, twice, and Form 1, once. The predominance of Form 7 may have been due in part to the more frequent presence of oat plants in other parts of the nursery having the resistance of White Russian than those

resistant to Forms 3 and 7 and the consequent greater increase of inoculum of the latter types.

PLATE II



A B C D

Stem rust reactions on stems of adult plants
A, Gopher; B, Susceptible segregate; C, Resistant segregate; D, Rainbow.

In the course of F_3 classification for rust reaction in the field, plants in segregating families were noted, having what appeared to be a mixture of pustule types, or, large and small pustules. Seedling progenies from 50 such plants were tested for reaction to Physiologic Form 2. Forty-three of these progenies were homozygous for susceptibility, six were segregating and one was resistant. These results indicate that the occurrence of small and large pustules on single plants may be due to developmental causes and has no fixed relation to the rust genotype of the plants. An unsuccessful effort was made to establish rust cultures from the small and large pustules to determine whether the same forms of rust existed in each of these.

Straw Strength and Blast Studies

The apparatus described by Clark and Wilson was used in the studies reported here. In 1932 culm diameter and breaking strength were determined for several groups of random and selected F_2 plants and also for the parents. The mean values and standard errors are given in Table 8. In Table 9 the mean values for culm diameter and breaking strength of parents and progenies may be compared on the basis of the standard errors of their differences.

The separate groups, as indicated by Arabic numbers in Tables 8 and 9, consist of plants grown in the same area of the nursery. Comparison of parents and selected or unselected progenies may be made, therefore, directly within groups. Different groups may be compared, tho grown in adjacent areas. Group 2 consists of plants grown in the stem-rust nursery, being those taken at random for rust studies. Group 3 consists of plants taken from an adjacent area, not artificially rusted but in which some rust was present. Groups 2 and 3 were grown in 1932. Group 1 was grown in the stem-rust nursery in 1933. Plants designated as "selected F_2" were selected in the field as rust-resistant and possessing strong straw, as determined by springiness of the culms. The data indicate a slightly higher culm diameter and breaking strength for plants selected than for unselected plants. In the 476 F_2 plants classified for strength of straw by "feel" the following data were obtained for the strong- and weak-strawed classes, measuring culm diameter and using the breaking test:

	Mean culm diameter, mms.	Mean breaking strength, gms.
149 strong-strawed plants	3.86	1822.32
327 weak-strawed plants	3.60	1590.86

These values indicate that such characters may be approximately estimated by superficial observation at maturity in the field.

In Table 8 means and standard errors for culm diameter and breaking strength, with correlations between these two variables, are indicated. The data show considerable variation in the values of r obtained for comparable progenies. Gopher exhibits a higher average correlation between culm diameter and breaking strength than does Rainbow, tho this does not appear to be significant. The average correlations in selected and random progenies are very similar, indicating that rust susceptibility or resistance did not affect the relation of culm diameter and breaking strength noticeably in the tests made. The Gopher and Rainbow progenies in Group 4 were more severely lodged and the plants more mature than plants elsewhere in the nursery. This might account in part for the low correlations obtained in these cases.

The Gopher and Rainbow progenies in Group 5 were studied while the plants were yet quite green and the grain in the soft to medium dough stage. It is at about this time in the growth period that lodging commonly occurs. At this stage the correlation of culm diameter and breaking strength in Gopher was considerably higher than for Rainbow.

The means for culm diameter and breaking strength in Table 8 indicate closer resemblance of the progeny averages for culm diameter to Rainbow, while the breaking strength values also agree more closely with those for Rainbow in two of the three comparisons.

Table 8

The Means and Standard Errors of Culm Diameter and Breaking Strength and Correlations between Culm Diameters and Breaking Strength in Parents and Hybrids

Material	Number of plants or families	Culm diameter		Breaking strength		r	P values*
		Mean (mms.)	Standard error	Mean (gms.)	Standard error		
1. Random F_2	162	4.14	.03	967.90	29.81	.35	Below .01
a. Gopher	43	3.88	.07	976.74	40.66	.79	" "
b. Rainbow	49	4.21	.05	1308.20	40.80	.20	Exceeds .1
2. Random F_2	432	3.86	.02	1301.86	16.54	.54	Below .01
a. Gopher	50	3.47	.05	1100.00	34.41	.46	" "
b. Rainbow	50	3.89	.05	1336.00	33.79	.58	" "
Selected F_2	276	3.92	.02	1397.82	18.74	.42	" "
3. Random F_2	476	3.65	.02	1655.88	15.62	.54	" "
a. Gopher	60	3.43	.04	1580.00	36.88	.50	" "
b. Rainbow	60	3.69	.04	1670.00	33.61	.56	" "
Selected F_2	171	3.95	.02	1676.60	19.63	.49	" "
4. Gopher	59	3.91	.05	903.38	24.68	.20	Exceeds .1
Rainbow	82	4.19	.03	1068.30	22.21	.22	.05 to .02
5. Gopher	115	3.95	.03	729.56	31.16	.56	Below .01
Rainbow	113	4.13	.05	735.40	20.98	.29	" "
6. Culm diameter F_2 with F_3 means	102	4.02	.06	4.21†	.05	.09	Exceeds .1
7. Breaking strength F_2 with F_3 means	102	1319.60	15.23	1154.90†	30.44	.10	Exceeds .1

* Obtained from Fisher's table and represents the probability that the correlations could arise due to the errors of random sampling in an uncorrelated population. .05 point taken as upper P value for significance.

† F_3 mean for all families.

Lodging in the stem-rust nursery in 1933 was so uniform and complete that no differentiation for lodging between the parents or among the progenies could be observed. A study of the relation between physical measurements of the F_2 plants and lodging indices of the F_3 lines was therefore not possible. The relation of the culm diameter and breaking strength of F_2 plants with the means of their respective F_3 progenies was not significant, as is indicated by the value of the correlation coefficient. (6 and 7, Table 8.)

In Table 9 the means for culm diameter and breaking strength included in the previous table have been compared on the basis of their standard errors. The values of differences over their standard errors indicate that error in breaking-strength tests is higher, or differences between varieties in this respect are smaller, than for culm diameter.

In five comparisons of Gopher and Rainbow for culm diameter, Rainbow was significantly different from Gopher in each case. Differences in breaking strength between the parent varieties were significant in four of these instances.

Table 9

Significance of Mean Differences of Parents and Progenies, Using the Difference Divided by the Standard Error of the Mean Difference as an Indicator

Comparison	Culm diameter Difference/Standard error	Breaking strength Difference/Standard error
1. Gopher with Rainbow	4.79	5.75
Gopher with Random F_2	3.19	.19
Rainbow with Random F_2	1.37	6.73
2. Gopher with Rainbow	6.44	4.89
Gopher with Random F_2	7.9	5.29
Gopher with Selected F_2	8.85	7.60
Rainbow with Random F_2	.50	.91
Rainbow with Selected F_2	.62	1.60
3. Gopher with Rainbow	14.54	1.81
Gopher with Random F_2	4.93	1.89
Gopher with Selected F_2	10.98	2.31
Rainbow with Random F_2	.84	.38
Rainbow with Selected F_2	5.90	.18
4. Gopher with Rainbow	5.80	4.97
5. Gopher with Rainbow	3.47	.16
F_2 mean with F_3 mean	23.87	4.84

Note: A value of 2 may be taken as the minimum level of significance.

Comparing Rainbow and Gopher with random F_2 progenies, the data indicate non-significant differences between Rainbow and the progenies for culm diameter, whereas Gopher differs beyond chance

expectation when compared with the random progenies in all three cases. Gopher differs significantly in breaking strength from the F_2 progeny in two comparisons and Rainbow in one. Selected progenies compare with the parents in a similar manner as those taken at random.

The means of the F_2 progeny for both culm diameter and breaking strength differed significantly from the F_3 family means in which approximately 4,000 plants were tested. This is particularly true for culm diameter.

Length of the internode broken was not generally considered in the breaking tests. The relation of this factor to breaking was studied for 78 plants and the following correlations obtained:

	r	P
Culm diameter with breaking strength	.62	Less than .01
" " " internode length	.15	Exceeds .1
Breaking strength with " "	—.24	.02 to .05

The values of r obtained indicate that, even tho the distance between the rests on the apparatus used was constant, the longer internodes had lower breaking strengths.

Date of heading of 245 F_3 families was correlated with a blast percentage index of such families in the field in 1933. Since some of these lines were segregating, the values assigned represent approximations only. Blast percentage was read in classes of 5 to 30 per cent with 5 per cent intervals. The limits of this range represent the average values of Gopher and Rainbow, respectively. A correlation coefficient of .17 was obtained for the association between blast percentage and date of heading.

Using Fisher's t test for the value of r when n^1 is 245 one derives a P value of less than .01, which indicates a fair positive relation between percentage of blast and lateness of heading. The X^2 test for independence for these data gave a P value of .02 to .01.

Crown-Rust Studies

Seedling data.—The crosses studied in these experiments were:

	Generations		
Victoria x Double Cross II-22-220	F_1	F_2	F_3
" x Anthony	F_1	F_2	F_3
" x Minrus	F_1	F_2	
" x Rainbow	F_1	F_2	

It should be noted that progeny tests of phenotypic classification are not generally available since the crown-rust nursery data are for one season only. Preliminary studies of seedling reactions in the

greenhouse were made to determine their value in breeding for adult-plant crown-rust resistance.

The seedling studies of the susceptible varieties used in these experiments indicated that rust reactions vary from plant to plant of the same variety, tho reactions were generally of a susceptible or mesothetic type to the forms used. None of the other parental varieties showed the marked resistance of Victoria. In Table 10 the results of these tests are given. Class X is similar to Class 4 except that scattered necrotic areas resembling those caused by the rust fungus were present with the Class 4 pustule. The parents shown in the plates indicate these reaction classes.

Table 10

Greenhouse Seedling Reactions of Individual Plant Progenies of Varieties to Physiologic Forms of Crown Rust

Variety	Plant No.	Physiologic Forms							
		1	2	3	4	6	7	17	24
Victoria	1	0	0	2	1	0	1	0	0
	2	1	2	0	0	2	1	1	2
	3	0	1	1	1	1	0	0	0
	4	2	2	0	2	0	2	2	1
	5	0	1	2	0	2	0	0	1
Anthony	1	x	4—	4	x	4—	x	x	4—
	2	x	4—	4—	x	4	x	x	4—
	3	x	4—	4—	x	4—	x	4—	4—
	4	4—	4—	4—	x	4—	4—	4—	4—
	5	x	4	4—	x	4—	x	x	4
Minrus	1	x	4—	4—	4	4—	x	4—	4—
	2	x	4	4—	4	4	x	4—	4—
	3	x	4	4—	4	4	x	4—	4
	4	4—	4—	4—	4	3	x	4—	4
	5	4—	4	4—	4	4	x	4—	4
Rainbow	1	4—	4—	4—	4	4	4	4—	4
	2	4	4	4	4	4—	4	4—	4
	3	4	4	4—	4	4—	4	4	4
	4	4	4	4	4	4—	4	4—	4
	5	4	4—	4—	4	4	4	4	4
D.C. II-22-220	1	4	4—	4—	4	4—	4—	4—	4—
	2	4—	4—	4	4	4	4	4—	4—
	3	4	4—	4—	4	4	4—	4—	4—
	4	4	4—	4	4	4	4—	4—	4
	5	4—	4—	4	4	4	4	4—	4—

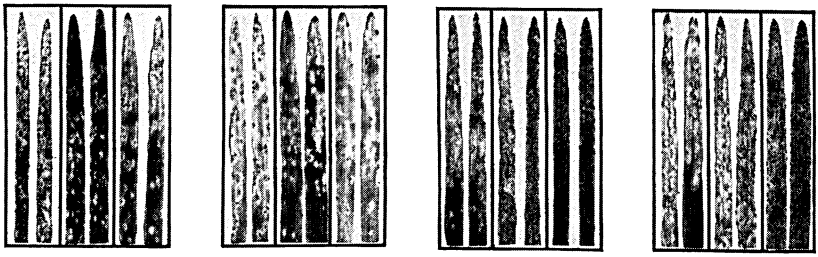
Note: 4— indicates scattered (few) pustules but of a 4 or susceptible type.

The F_1 reaction of seedlings was determined by growing such plants in the greenhouse and inoculating them with Physiologic Form 7, using the brushing method. Progenies of the parent plants were grown in the same series for comparison. Where reaction of the F_1 plant was dif-

ferent from that of the female parent, the material was assumed to be of hybrid nature. The following reactions were obtained in F_1 crosses:

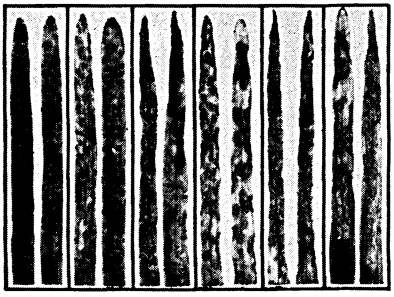
	No. of F_1 plants	Dominance
Victoria x D.C. II-22-220	6	Intermediate
" x Anthony	3	Resistance
" x Rainbow	3	Intermediate
Minrus x Victoria	6	Resistance

PLATE III



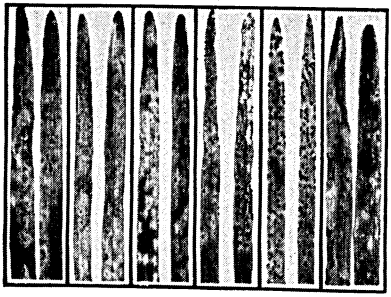
A B C D

Fig. 1. Reactions of parents and F_1's to Form 7, *P. coronata*
Left panel, female parent; central panel F_1; right panel, male parent of the respective crosses. A, Parents and F_1, Minrus x Victoria; B, Parents and F_1, Victoria x Anthony; C, Parents and F_1, Victoria x D.C. II-22-220; D, Parents and F_1, Victoria x Rainbow.



A B C

Figure 2



D E F

Figure 3

Fig. 2. Reaction of parents and F_2 seedlings of D.C. II-22-220 x Victoria to Form 7, *P. coronata*
Left panel, II-22-220; right panel, Victoria; central panels, F_2 seedling types.
A, Double cross, II-22-220; B, 4 types of progeny reaction; C, Victoria.

Fig. 3. Reactions of parents and F_2 seedlings of Victoria x Minrus to Form 7, *P. coronata*
Left panel, Victoria; right panel, Minrus; central panels, F_2 seedling types.
D, Victoria; E, 4 types of progeny reaction; F, Minrus.

Plate III, Figure 1, shows the reactions to Form 7 of parents and hybrids in these crosses. In the Anthony and Minrus x Victoria hybrids resistance appeared to be distinctly dominant. In the Rainbow and D.C. II-22-220 hybrids the F_1 type was intermediate. Small varia-

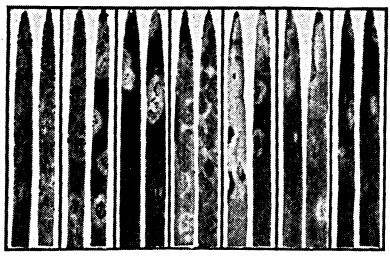
tions in the Victoria parent reaction may be noted in the illustrations. The purity of the inoculum of Form 7 used in these inoculations is not certain, slight mixtures of other forms perhaps being present. This circumstance may be the reason for the occurrence of occasional large pustules of a susceptible type on leaves otherwise resistant in appearance.

The reactions of F_3 seedlings from 24 F_2 plants of Anthony x Victoria were observed, using Forms 1, 2, 3, 4, 6, 7, 17, and 24. For some undetermined reason the germination of apparently normal grains of these progenies was approximately 20 per cent, and too few seedlings representing each F_2 plant were obtained to permit sufficient numbers for satisfactory classification of rust types. The seedlings varied in reaction from a 1— to a 4 type, with most plants occurring in resistant classes. F_3 families that were rather uniform in reaction to one rust form reacted in a similar manner to other rust forms, and those F_3 lines segregating for reaction to one form appeared to segregate for reaction to other forms also. Types of reaction obtained using Form 7 are shown in Plate III, Figure 2.

Eighty-one F_3 families of D.C. II-22-220 x Victoria were grown in the greenhouse and inoculated in the seedling stage with a field collection of crown rust made in 1933. This inoculum was not identified as any specific form or composite of forms. No families breeding true for a Class 3 or Class 4 reaction, similar to that of the susceptible parent, were found. Further, most families in this group contained some seedlings having the Class X reaction. Thirteen families appeared to be breeding true for the Victoria type, while of the 68 remaining families only two gave segregations resembling complete susceptibility. Most seedlings were classified as 1 or 2 in type. The variation in this progeny is shown in Plate IV, Figure 1. The plants were grown under rather unfavorable light conditions both as to season and location, and the reactions obtained were different, undoubtedly, from the type of reaction that would be expected in normal light. These types may be compared with other figures showing seedling reactions under good light conditions, tho the inoculum in these cases was different. Plate IV, Figure 2, illustrates types of seedling reactions of Anthony x Victoria F_3 progeny and parents.

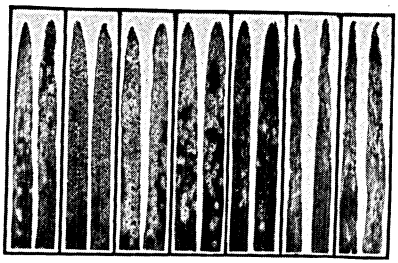
In nine F_2 seedling progenies of Victoria x D.C. II-22-220, consisting of approximately 16 of each progeny inoculated with Form 7, the majority of the plants were of resistant and intermediate types. In only one of these families were seedlings of the susceptible parent type noted. Plate III, Figure 2, shows the types of reaction obtained in these crosses. In Plate III, Figure 3, a similar progeny of Victoria x Minrus is shown. In this cross, as in the previous one, most individuals occurred in intermediate and resistant classes.

PLATE IV



A B C

Figure 1



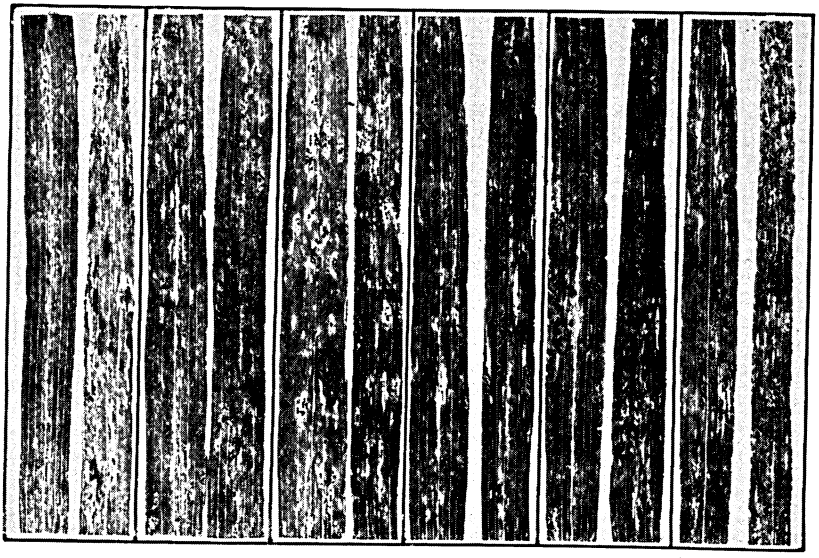
A B C

Figure 2

Fig. 1. Seedling reactions of D.C. II-22-220 x Victoria F_3 and parents to field collection of *P. coronata* made at U. Farm, 1933

A, Left panel, II-22-220; B, Central panels, five types of progeny reactions; C, Right panel, Victoria. (Plants grown in poor light.)

Fig. 2. Seedling reactions of Anthony x Victoria F_3 and parents to Form 7, *P. coronata* A, Left panel, Anthony; B, Central panels, five types of progeny reactions; C, Right panel, Victoria. (All plants grown in good light.)



1 2 3 4 5 6

Fig. 3. Six classes for crown-rust reaction of adult plants made in field nursery, 1933 Classes 1-3 show some necrosis. Increased amounts of rust accompanies higher numbers.

Field reaction.—Data for adult plants were obtained in the crown-rust nursery in 1933, and data on reactions of progenies of these plants are not available. Tho the reactions of F_1 plants were somewhat uncertain because of poorer growth and premature ripening, compared with the remainder of the nursery, the reactions noted in Table

11 are believed to be worthy of consideration. Since some F_1 plants of each cross grown showed an intermediate rust reaction, plants in the F_1 progenies having the female parent character are not included in the table.

Table 11

Adult Plant Classification to Crown Rust of Parents and F_1 Plants in the Rust Nursery

Parent or Hybrid	Adult Plant Rust Class					
	1	2	3	4	5	6
Victoria	9					
F_1		3	3			
D.C. II-22-220				13		
Victoria	15					
F_1			3	5		
Rainbow		10	5			
Victoria	12	2				
F_1		1	10			
Anthony				24		
Victoria	14					
F_1	1	4	5	3		
Minrus				19		

Numbers represent plants in each class.

The classification of F_1 plants indicates, as for the seedlings, an intermediate condition for rust reaction in the Minrus or D.C. II-22-220 x Victoria hybrids. The reactions of the Anthony or Minrus x Victoria F_1's are also intermediate, tho the F_1 seedlings observed indicated resistance to be completely dominant. The exceptional F_1 individuals of Victoria x Minrus, classified as 1 or 4, were included since these particular plants were supposedly different in reaction in each case from the female parent.

The numbers of parent plants, tho few, indicate the reactions of progenies of actual parent plants used and the variation in classification of these plants.

In Table 12 are shown frequency distributions of F_2 progenies of Victoria with D.C. II-22-220, Anthony and Minrus. Each horizontal row represents one progeny. The numbers available in the F_2 crosses listed are small. The field stand of plants obtained was very thin, partly due to unfavorable weather conditions in early growth stages and perhaps in part to the nature of the material. Approximately 20 per cent of seeds planted produced plants. The two groups of Victoria x D.C. II-22-220 crosses (1 and 2) were made since the recorded parent reactions of the susceptible parent were somewhat different between these groups, probably due to location in the nursery.

Table 12

Distribution of Adult F_2 Progenies and Parents Grown in the Field Nursery into Crown-Rust Reaction Classes

Progeny or Parent	Rust Classes						
	1	2	3	4	5	6	Totals
1. Victoria x D.C. II-22-220	20	34	19	1			74
and reciprocal	14	28	8	1	1		52
	3	8	5				16
	4	9	6	1			20
	10	26	6	2		7	51
	20	28	33	16	4		101
	12	24	15	3			54
	7	19	3	4			33
	5	11	8	2			26
	6	15	15	6		4	46
Victoria	26	13	7				46
D.C. II-22-220			2	13	20	24	59
2. Victoria x D.C. II-22-220	3	4	5		1		13
and reciprocal	11	29	13	22			75
	5	7	3	1			16
	1	9	7	1			18
	16	23	13	3			55
	16	8		1			25
	5	7	5	1			18
	5	8	6	2			21
	12	5	4	2	1		24
	3	10	4	9			26
	5	8	6	2			21
Victoria	41	3	1				45
D.C. II-22-220			1	40	25	11	77
3. Anthony x Victoria	21	22	3	2			48
	41	46	14	9			110
	16	22	7	2			47
Anthony	2	1	6	30	3		42
Victoria	29	9					38
4. Minrus x Victoria and re-	17	40	34	5	5	2	103
ciprocal	16	30	25	11	13	2	97
	46	68	43	7	1		165
Minrus				15	10	26	51
Victoria	27	6	2				35

The results given in Table 12 indicate some of the difficulties of attempting to explain the results on a definite genetic factor basis. The Victoria parent gave a considerable number of plants in Class 3, and the F_1 adult plants for the most part gave an intermediate reaction. The greater part of individuals in Class 3 are probably somewhat resistant, as only three plants out of 136 in D.C. II-22-220, and none in Minrus, gave as low a reaction as Class 3. The results with Anthony are difficult to explain, as eight plants out of 42 were in Class 3 or in the more resistant groups. An attempt to place such results on a definite factor basis does not seem to be justified.

Table 13

Distribution of Adult F_3 Progenies and Parents of Victoria x D.C. II-22-220, Grown in the Field Nursery, into Crown-Rust Reaction Classes

Progeny	Rust Classes						Progeny or Parent	Rust Classes					
	1	2	3	4	5	6		1	2	3	4	5	6
Victoria x D.C. II-22-220	2	5	3					8	6	2	1		
		6	2					2	4	3			
	4	8	2	3				3	12	2			
		6	2					3	6	1			
	6	5	4	1				3	1				
	12	6						1	3	1	4	1	
	1	2	2					4	2	1			
	1	3	2					2	2		3		
	4		3		3			1	1	3			
	2	7	1	1	2			2		1	6		
	2	7	1					1	2		1		
		5	2		1			5	4				
		3	3					6	5	2			
		4	3	5				1	1	2	2		
		2	3					3	1	2	2		
	1	4	3					4	6	1			
		4	4					2	2	1			
	3	5	1	1				4	5	1			
	4	2	5	4	1			2	7	2	1	1	1
	5							2	1	1	7	5	
	1	4	2	1				3	1	2	2		
		5	4	2				4		1		1	
	1	6		1	1				1	2	2	2	1
	5	6	3	2					1	2	2	7	4
	1	4	8	1					1	5		2	
	6							5	4	1	2	1	
	5	6								6	2	2	2
	1	5	1				Victoria	47	12	4	2		
	1	2	2	2		1	D.C. II-22-220			1	63	22	16

F_2 plants from the cross of Victoria x D.C. II-22-220 were grown in the greenhouse and F_3 progenies classified for crown-rust reaction under field conditions. The data are given in Table 13. In this case, out of 65 plants of Victoria, four were placed in Class 3 and two in Class 4. Of the 56 F_3 families grown, only one resembles the Double Cross parent in reaction and it had a greater preponderance of plants in Class 3 than the Double Cross parent.

The classification of 26 F_3 progenies of Anthony x Victoria and parents are shown in Table 14. Tho numbers are few, one of these groups resembles Anthony while several give distributions similar to that for Victoria.

Plants of the hybrid progenies in the crown-rust nursery were harvested as they ripened, harvests being made on eight successive dates from July 27 to September 16. The intervals between harvests were 2, 2, 3, 2, 7, 7,and 28 days.

Table 14

Distribution of Adult F_3 Progenies and Parents of Anthony x Victoria, Grown in the Field Nursery, into Crown-Rust Reaction Classes

Progeny	Rust Classes						Progeny or Parent	Rust Classes					
	1	2	3	4	5	6		1	2	3	4	5	6
Anthony x Victoria	8	4	3				Anthony x Victoria	1	4				
	2	2						9	4	3			
	9	4	1					4	5				
	1	1	1	3	1			6	2				
	2	3						5	5	3			
	9	5	1		1			4	1				
	6	4	1					4	4	1			
			1	1	1			8	5				
	3	2						5	6				
		1	2	2	1			2	5	2			
	8	1	1					7	6	1			
	1	2	2					4	12	1			
	4	2	2				Anthony			1	15	14	11
	4	1					Victoria	13	3	4			

In Table 15 the results of X^2 tests for independence of crown-rust reaction and date of ripening are given for the progenies listed in Table 12. The P values for the Victoria x D.C. II-22-220 progenies clearly indicate lack of independence in both F_2 and F_3 generations. The deficiencies are of the early-maturing, resistant types. In the Anthony x Victoria progenies there is reasonable agreement with an independence hypothesis. The Minrus x Victoria segregation fails to be in satisfactory agreement with numbers expected on the basis of independence. The contributions to X^2 in this case appeared to be nearly at random, tho early and resistant plants were too few.

Table 15

X^2 Tests for Independence of Crown-Rust Reaction and Date of Maturity in Hybrid Progenies

Progeny		X^2 Values	Degrees of freedom	P
Victoria x D.C. II-22-220	F_2	93.4906	21	Less than .01
do	F_3	101.9775	21	" " .01
Anthony x Victoria	F_2	7.7216	7	.50 to .30
do	F_3	19.7255	12	.10 to .05
Minrus x Victoria	F_2	65.5028	14	Less than .01

DISCUSSION OF RESULTS

Studies on the inheritance of reaction to *Puccinia graminis avenae* in the cross of Gopher x Rainbow indicate that resistance and susceptibility to Physiologic Forms 1, 2, 3, 5, and 7 are dependent on a single-factor pair. This factor in Rainbow acts as a dominant to the Gopher

factor for moderate resistance to Forms 1, 2, and 5 and susceptibility to Forms 3 and 7. The segregating classes for these five forms were unmistakable. Both parents were susceptible to Physiologic Form 8, but in the F_3 progenies seedlings of resistant types were observed. Since the F_2 progeny reaction to Form 8 is unknown, the genetic nature of such resistant types in the segregating F_3 progenies is questionable. A possible mixture of other physiologic forms of rust with the inoculum of Form 8 used is not considered as sufficient explanation for the results obtained. The fact that families heterozygous to Forms 1, 2, 3, 5, and 7 produced such individuals, while those homozygous failed to do so, indicates that the same factors, or others closely linked, control this reaction.

The classification of reaction to Form 9 was less distinct than for other forms. Families homozygous resistant and heterozygous to Forms 1, 2, 3, 5, and 7 behaved similarly to this form. Homozygous susceptible families for reaction to these forms showed less variation than other progenies. These families tended to be more like the Gopher parent which was moderately resistant to Form 9. Such results would be expected if the same factor were acting, plants carrying this factor being susceptible to Forms 1, 2, 3, 5, and 7 when compared with Rainbow, but resistant to Form 9 when compared with the Rainbow parent.

The reactions of the Gopher and Rainbow parents to Physiologic Forms 4 and 6 were of a susceptible nature. No progenies resistant to these forms were obtained.

The data on rust reaction indicate a single-factor pair to be involved in the segregation. With the exception of Dietz (7) (8), Welsh (35) and Gordon and Welsh (17), investigators have obtained 3:1 ratios in crosses of strains differing in stem-rust reaction. Results indicate the existence of a series of allelomorphs for stem-rust reaction. If reaction to all forms were controlled by a series of allelomorphic factors at the same loci of a single pair of chromosomes, it would be impossible to combine factors controlling resistance to different forms into a single homozygous individual. Gordon and Welsh (17), however, concluded that resistance to Form 4 was inherited independently of resistance to Forms 1, 2, 3, 5, and 7, tho 3:1 ratios were obtained in studies of reaction to Form 4.

From the results thus far obtained on alternative inheritance, it appears unquestionable that a series of multiple allelomorphs controlling rust reaction exists, altho it seems apparent that all factors for stem-rust reaction are not in this series.

Inheritance of rust reaction was independent of other plant characters studied, and true breeding families having all combinations of rust reaction with other characters should be obtainable. The close asso-

ciation of lemma color, awn development, and basal bristles, as reported by many workers, also existed in the Gopher x Rainbow progeny. Yellow lemma color appears to limit awn development directly or to be closely linked with an inhibiting factor.

A fair correlation exists between culm diameter and breaking strength of straw, as might be expected on a strictly mechanical basis. Tho Gopher is considerably more resistant to lodging under field conditions, the strain of this variety used in these experiments had a smaller culm diameter and lower breaking strength than the Rainbow parent. This difference was less prominent in green than in mature plants. Physical measurements of Rainbow more closely approached progeny averages in the Gopher Rainbow cross than did those of the Gopher parent. The absence of significant correlation between F_2 culm diameters or breaking strengths with mean culm diameters or mean breaking strengths of F_3 progenies indicates the inadequacy of tests of these values in measuring any heritable quality of the culm in this respect. No direct relation of culm diameter or breaking strength to lodging could be measured since differential lodging indices could not be obtained. Selection of plants for strength of straw by "feel" appears to be a satisfactory means of eliminating plants of small culm diameter and low breaking strength. It is believed that factors other than those studied may play a more prominent part in determining the lodging reaction of oat plants.

Resistance to crown rust appears to be a dominant or partially dominant character, both in seedlings and adult plants. The validity of the rust classes established for seedling and adult plant reactions was not generally substantiated, since progeny tests of such classes were not made. This fact makes the basis for a genetic explanation of the segregations somewhat questionable. It is of interest to note that crown-rust resistant plants that headed as early as the early maturing parent were rather easy to obtain.

In a general manner, at least, reactions of hybrid material, to crown rust, as adult plants in the field are similar to those obtained for seedlings in greenhouse tests.

The crown-rust resistance of the Victoria parent used in the crosses discussed appears to be associated with lateness of maturity in some crosses, while in others no such relation is indicated. This association is of a similar nature to that occurring for these two characters in the Victoria parent.

SUMMARY

1. Progenies of crosses of two varieties of oats differing in reaction to physiologic forms of *Puccinia graminis avenae* were studied in the F_2 and F_3 generations for rust reaction to individual forms of stem rust and for other characters.

2. Stem-rust resistance was inherited as a dominant character, and evidence is given to show that a single-factor pair is active in its determination. The resistance of Rainbow to Physiologic Forms 1, 2, 3, 5, and 7 was dominant in the progeny. The results obtained for segregation to Forms 8 and 9 were inconclusive regarding the manner of inheritance, tho the data indicate that the same factor pair influences the reaction to these forms. No families resistant to Forms 4 or 6 were obtained.

3. Upon the basis of these and previous studies made by other workers the probable existence of a series of multiple allelomorphs controlling reaction to *Puccinia graminis avenae* is indicated.

4. Stem-rust resistance was inherited independently of lemma color, awn length, strength or presence, basal hairs, blast, culm diameter, or breaking strength of straw.

5. Seedling and adult plant reactions to Forms 1, 2, 3, 5, and 7 were in complete agreement.

6. The use of the breaking strength of straw test as a means of distinguishing plants having an inheritable advantage in this respect is unjustified, based upon these experiments. Other factors than culm diameter and breaking strength are important in the distinction of strains resistant to lodging.

7. Percentage of blast in F_3 families was significantly correlated in a positive manner with lateness of heading.

8. Resistance of F_1 plants to crown rust, *Puccinia coronata,* was dominant or intermediate in the seedling stage and intermediate in the adult plants in four crosses observed.

9. Segregation in the F_2 generation of crosses of Victoria with Double Cross II-22-220, Minrus and Anthony indicated that early-maturing types resistant to crown rust could be obtained from these crosses. The small number of completely susceptible families in F_3, in crosses of Victoria with Double Cross and Anthony, indicates that more than a single factor is involved or that susceptible types were eliminated due to some type of sterility.

10. Crown-rust resistance was associated to some extent with lateness of maturity in progenies of Victoria x D.C. II-22-220. This relation was less marked or absent in crosses of Minrus and Anthony with Victoria.

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