THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Thesis

The undersigned, acting as a Committee of the Graduate School, have read the accompanying thesis submitted by James Bishop Harrington for the degree of Master of Science. They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science.

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Date May 27, 1922

THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Examination.

This is to certify that we the undersigned, as a committee of the Graduate School, have given James Bishop Harrington final oral examination for the degree of

Master of Science

We recommend that the degree of

Master of Science

be conferred upon the candidate.

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Date May 27, 1922

THE MODE OF INHERITANCE OF RESISTANCE TO PUCCINIA GRAMINIS IN RELATION TO SEED COLOR IN A CROSS BETWEEN TWO VARIETIES OF DURUM WHEAT.

A THESIS

Presented to the Faculty of the Graduate
School of the University of Minnesota
in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

By

JAMES B. HARRINGTON

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INTRODUCTION.

It has long been recognized that the production of economically desirable varieties of wheat resistant to Puccinia graminis tritici (Erikss. & Henn.) would be of great economic value. Until recently hybridization experiments with this end in view were based upon a very incomplete knowledge of both the pathogene and the nature of the inheritance of resistance, consequently satisfactory results were not obtained. It has been recently learned that there are several biologic forms of wheat stem rust. This has been of much value in placing breeding studies on a definite basis. The benefit of a knowledge of the mode of inheritance of certain desired economic characters has served to help the breeder in outlining breeding plans. Varieties belonging to various of the wheat species have been discovered which are resistant to certain biologic forms of stem rust. By hybridization it is hoped to combine in one variety resistance to all biologic forms. The mode of inheritance of the resistance or susceptibility to particular biologic forms must be made known before it can be stated that resistance to all forms of stem rust can be combined in a single variety. The present problem was attacked with the hope of aiding in a determination of the possibility of obtaining a desirable economic type of wheat resistant to all known biologic forms of stem rust.

REVIEW OF PREVIOUS WORK.

Although wheat stem rust was recognized in ancient times as an enormously destructive disease (Levine, 1919), there was little definite knowledge of the pathogene's life cycle and hosts until within the last few years. The phenomena of physiologic specialization of parasitic fungi was pointed out by Schroeter in 1879, according to Reed (1918). Eriksson was the first to show definitely that biologic specialization occurred. This was in 1894 when he was working with Puccinia graminis. He showed that what was usually considered as one species, attacking all of the common cereals, in reality consisted of several pathologic strains or biologic races. Hitchcock and Carleton (1894) also studied biologic specialization. They observed that there was little danger of rust from one cereal infecting another. Carleton (1904) concluded that the forms of black stem rust on wheat, barley, and some grasses were identical and that the form on Agropyron occidentale was distinct from them. A few years later Freeman and Johnson (1911) stated that there were eight distinct biologic forms of Puccinia graminis.

For some time it was generally believed that biologic forms might change rather rapidly as a result of host influence. Ward (1902) first suggested this possibility. He concluded from his work with P. dispersa that biologic forms were not necessarily fixed but that they could be transferred from one variety of brome to a third variety by means of a second variety of "bridging host". Salmon (Stakman, E.C., Parker, J.H., and

Piemeisel, F.J., 1918), Freeman (1902), Freeman and Johnson (1911), Johnson (1911), and Evans (1911) confirmed Ward's results after working with P. graminis.

Evans (1911) decided that bridging made the development of resistant varieties of wheat rather uncertain. However, more recent work with P. graminis by Stakman, Parker and Piemeisel (1918) and Stakman, Piemeisel and Levine (1918) has shown that bridging either does not occur or is relatively unimportant. That is to say, biologic forms of rust appear to be quite stable. For example, Form 1 has remained quite constant in character since September 1915 at the Minnesota station. Several other forms have been kept now for three years without any indication of change regardless of the hosts they have been cultured on.

Previous to 1916 it was generally believed that only one form of black stem rust attacked wheat. It was established, however, by Stakman and Piemeisel (1916, 1917) that more than one form of Puccinia graminis tritici* existed. They described a second form P. graminis tritici compacti. Soon after, Melchers and Parker (1918), Levine and Stakman (1918), and Stakman, Levine and Leach (1919) showed that there were a number of biologic forms of P. graminis tritici. By January 1, 1922, a total of 37 different biologic forms of P. graminis tritici had been isolated at the Minnesota station by Stakman and Levine.+ No one

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* The name "P. graminis tritici" is used through this paper for wheat stem rust in general, which includes many biologic forms.

+ Unpublished results.

form can attack all varieties of Triticum species and no wheat variety has been found to be resistant to all rust forms, except Khapli, a T. dicoccum variety.

The exact distribution of each biologic form is not known. Perhaps, not half of the 37 forms are present in any one wheat-growing vicinity. For example, only 11 forms had been collected up to December, 1920, in Western Canada according to Miss Newton (1920). However, since it is very probable that the spread of each form into new districts is only a matter of time, the problem of breeding for resistance means working for a variety resistant to all known forms.

The study of disease resistance in wheat dates back over a century. Thomas Knight, in 1815, suggested that disease resistant varieties might be raised. Farrar, in 1889, stated that susceptibility to rust was hereditary in wheat. Biffin (1906) crossed Red King, a variety susceptible to Puccinia glumarum, with Burt, a resistant variety. The F_1 was susceptible and the F_2 segregated into susceptible and resistant in a 3:1 ratio. Later, Biffin (1907) stated that the relatively immune hybrid forms of wheat bred true and that the immunity was independent of any discernable morphological character, that is, the factors for resistance were inherited independently of other factors. Recently, Biffin (1917) has reported the production of a rust resistant wheat which likewise possesses other desirable economic characters.

Vavilov (1914) was able to group definitely the wheat subspecies according to their reaction to Puccinia triticina. The use of inter-species crosses in breeding for rust resistance is liable to some complication owing to the linkage of certain factors (Freeman, 1917; Hayes, Parker and Kurtzweil, 1920) such as durum character and rust resistance. Some excellent results have been obtained in breeding for resistance (Orton, 1918) but the problem is rarely as complicated as is the case with stem rust of wheat. Gaines (1920) crossed two varieties of wheat highly resistant to bunt and obtained in the F_2 some plants more susceptible than either parent and a large per cent of immune plants. He concluded that the two varieties had different factors for resistance. Garber (1921) found that resistance to P. graminis avenae was a dominant character, a ratio of 3 resistant plants to 1 susceptible being obtained in F_2.

In 1919, Hayes, Parker and Kurzweil (1920) found that in crosses of varieties of T. vulgare with varieties of T. dicoccum resistance was dominant. In crosses of T. vulgare with T. durum, susceptibility was a dominant and in F_2 there was strong linkage between rust resistance and the durum character, however, some crossing-over occurred. It was apparent that there was a possibility of transferring the resistance of durum or emmers to common wheats.

Puttick (1921) studied the reaction of the F_2 generation of a cross between a common and a durum wheat to two biologic forms of P. graminis tritici to which these varieties reacted reciprocally. F_2 seedlings were inoculated with one rust and later the infected leaves were cut off and the plants were inoculated with a second rust form. All gradations between complete susceptibility and immunity to both forms of rust were obtained. Some of the progeny appeared to be resistant to both forms of rust.

More recently, Melchers and Parker (1922) found that a single factor was responsible for the resistance in crosses of Kanred with Marquis, Preston and Haynes Bluestem which were inoculated with a single form of rust. Segregation in F_2 was in a 3:1 ratio of resistant and susceptible plants. The results were verified by carrying the study through the third generation.

Aamodt (1922) studied the inheritance of resistance to several biologic forms of P. graminis tritici in a cross between Kanred, a winter wheat, and Marquis, a spring-sown variety. Kanred is resistant to a number of biologic forms whereas Marquis is susceptible to most of them. F_3 seedling plants inoculated with a form of rust to which Kanred was immune and Marquis susceptible, proved either resistant or susceptible. Families homozygous for spring habit of growth and for resistance to all the forms of rust that Kanred was resistant to were obtained in the F_3. Here a single factor apparently determined the reaction to 11 biologic forms.

Of the 37 known biologic forms of stem rust, 21 were found in the northwestern spring wheat area*. The most recent disease-resistant breeding work at the Minnesota station shows the possibility of synthetically producing a desirable vulgare variety of wheat that will be resistant to all of these biologic forms (Hayes and Stakman, 1921). This is to be accomplished by means of several crosses and double crosses between varieties having the desired resistance and those having the necessary bread wheat qualities for yield, baking quality, etc. In

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* Unpublished results of Stakman and Levine.

connection with this problem a fairly extensive knowledge of the mode of inheritance is most important.

The object of the work described in this paper was the determination of the mode of inheritance of rust resistance in relation to seed color in a cross between two durum varieties which react differently to three biologic forms of <u>P. graminis tritici</u>.

MATERIALS AND METHODS.

Seedling plants from each F_3 family* of crosses between Mindum (Minn. No. 470), a white-seeded selection from Arnautka (<u>Triticum durum</u>), and D5, a red-seeded durum variety selected at the North Dakota station, were inoculated, in the greenhouse, with three biologic forms of <u>Puccinia graminis tritici</u>. The crosses were made in 1920 and the F_1 generation was grown in the greenhouse at Washington, D.C., during the winter of 1920-21. The F_2 generation was grown in the plant breeding nursery at University Farm during the 1921 season, the plants being harvested individually. The material was a part of that which was being used for the purpose of obtaining resistant wheats for growing in the Northwest, a problem being cooperatively investigated by the sections of Plant Breeding and Plant Pathology of the Minnesota Experiment Station and the Office of Cereal Investigations of the United States Department of Agriculture. The individually harvested F_2 plants were furnished to the present writer. The biologic forms were a part of those which were bwing studied by Mr. M.N. Levine.

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* The term "F_3 family" is used in this article for the seedling plants arising from seed of a single F_2 plant.

The first rust form, designated as Form 17, was collected at Madison, Wisconsin, in July, 1921. Previous to the time it was used for this problem, it had been cultured through approximately four generations of urediniospores and had appeared quite consistent in its parasitic capabilities. Four succeeding generations have revealed in it no tendency toward change. Mindum is highly susceptible to this form, but D5 is at least partially resistant.

The second form, known as Form 1, was collected at St. Paul, Minnesota, in June, 1918. It had been cultured through approximately thirty uredospore generations and there was no indication of a change in its parasitic capabilities. Mindum is decidedly resistant to this form, whereas D5 is normally susceptible.

The third form, designated as Form 34, was collected at Potchefstroom, South Africa, in April, 1921. When it was received at the Minnesota station it was evidently mixed with two other forms. The separation of these forms was not completed until December, 1921. Since then five generations have been produced without any indication of a change in the constancy of the form. In contrast to the reactions with Form 1, Mindum is quite susceptible to Form 34 and D5 is resistant.

Plants of each F_3 family were grown in six-inch pots in the greenhouse, one family per pot, with normally from 10 to 15 plants per pot. All pots of soil were steam sterilized immediately before use. The seed was all planted at a uniform depth. A large proportion of the hybrid seed, as well as of the parent seed was badly infected with Helminthosporium, consequently the number of seed planted was not a definite indication of the number of healthy seedlings produced, and the number of plants per pot sometimes fell below ten. The seedlings were grown in a seedling section of the greenhouse in which no rust infected plants were kept. When they were about three inches high, they were inoculated with fresh uredospores of one of the three forms used. Only one rust form was worked with at one time. The pots were then placed in an incubation chamber for 40 to 48 hours with a number of check pots of the parent varieties inoculated in the same way. Pots of inoculated plants were kept on greenhouse benches during the period of rust development. The three forms of rust were kept on well separated benches to avoid contamination of one by another. An attempt was made to keep the temperature, moisture, and light condition the same for all pots. The methods used were essentially the same as those described by Stakman and Piemeisel (1917).

Notes on the character of infection with both forms were taken from 15 to 19 days after the date of inoculation. The amount and rapidity of rust development was found to vary in response to environmental conditions. However, the character of infection was found fairly constant within certain limits regardless of external influences.

The F_3 seedling plants were inoculated in sets of about 25 to 40 pots each. The total interval during which results were being recorded for the reaction to any one biologic form was approximately two weeks. In addition to running check pots of the parent varieties with each set of hybrid pots a complete set of "differential" varieties was inoculated at the commencement of work with each form and another set when the work was completed. In this way a complete check on the identity of the form being used was obtained. The differential varieties were as follows: Little Club, Marquis, Kanred, Kota, Arnautka, Kubanka, Acme, Einkorn, Emmer, and Khapli.

The percentage of infection obtained was on the average very satisfactory. Of a total of more than 9600 plants which were inoculated, 675 showed no infection. This figure includes all plants like those of Kanred which are immune to certain biologic forms yet do not show hypersensitive flecks on the leaves and consequently cannot be classed as immune, without a second later inoculation being made.

In recording the types of infection the symbols prepared by Stakman and Levine in their work on biologic specialization were used (See Table 1).

Since the practical importance of results must necessarily be paramount in such a problem as this, the types of infection should be interpreted on the basis of their meaning in terms of field resistance or susceptibility. Types 0, 1, and 2 without doubt show resistance while X- and 3 types of greenhouse infection have been shown to indicate resistance under field conditions.* On the assumption that these five types indicate resistance they are grouped together, and any F_3 families showing types of infection wholly within this class are considered resistant as shown in the column headed "Resistant" under "Classes of Infection".

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* Unpublished results of cooperative rust breeding work carried on at the Minnesota station.

Table I.-- Explanation of Symbols Used to Indicate Types of Infection of Wheat Varieties by *Puccinia graminis tritici*.

0	IMMUNE. Definite hypersensitive areas present but no uredinia developed.
1	VERY RESISTANT. Uredinia minute and isolated; surrounded by sharp, continuous, hypersensitive areas; hypersensitive areas lacking uredinia may also be present.
2	MODERATELY RESISTANT. Uredinia isolated and small to medium in size; hypersensitive areas present; pustules often surrounded by green islands.
3	MODERATELY SUSCEPTIBLE. (Probably resistant in the field). Uredinia medium in size; coalescence infrequent; development of rust somewhat subnormal; true hypersensitiveness absent; chlorotic areas, however, may be present.
X-	RESISTANT TO MODERATELY SUSCEPTIBLE. (Probably resistant in the field). Combinations of two or more of the foregoing types, excepting 0 with 1 which is classed as 1.
4-	SUSCEPTIBLE. Uredinia medium in size, usually coalesced; hypersensitiveness absent; chlorotic areas seldom present.
4	VERY SUSCEPTIBLE. Uredinia large or varying from small to large, numerous and confluant; hypersensitiveness entirely absent but chlorosis may be present.
X+	MODERATELY SUSCEPTIBLE TO VERY SUSCEPTIBLE. (Probably susceptible in the field). Combinations of one or more of types 0, 1 and 2 with one or more of types 4- and 4.

Note: These descriptions of types of infection are based on recent unpublished results of Stakman and Levine.

Similarly X+, 4 and 4 are all considered as indicating susceptibility although it has not yet been satisfactorily established that X+ is a susceptible type. The heterozygous F_3 families showing a decided preponderance of resistant plants were classed as near-resistant and those with a strong majority of susceptible plants were classed as near-susceptible. All heterozygous F_3 families with approximately equal numbers of susceptible and resistant plants were placed as heterozygous.

The interpretation of results for the preliminary work with Form 17 as well as for the later work with Forms 17, 1 and 34 was made on the basis of these five classes. The important point in this connection is that plants showing types of infection from 0 to 3 were considered resistant and those showing types from X+ to 4 were considered susceptible, regardless of form of rust used.

Selection of Biologic Forms to Use: In October 1921, about 20 of the 37 known biologic forms were available in the greenhouse. At that time only a few forms had been run to D5 and the only one of these showing a differential reaction on Mindum and D5 was Form 17. The increase of that form was accordingly commenced at once. Meanwhile, pots of D5 were inoculated with each of the other forms of rust as rapidly as inoculum became available. Form 29 looked promising and was therefore increased for use. Further tests of Mindum and D5 to Form 17 gave variable results, consequently the idea of using that form was dropped. Stakman and Levine have found* that the durum

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* Unpublished results of Stakman and Levine.

varieties in general give less consistent results than vulgare varieties.

A form collected in Wisconsin in 1921 seemed to be very similar to Form 17 except that the reaction of D5 appeared more constant. The indications were that it was Form 37. This was increased in anticipation that it would prove suitable. At about this time the reaction of D5 to Form 29 was uncertain and Mindum continued to give rather indefinite X type infections, therefore this form was not considered further.

When the supposed Form 37 was sufficiently increased preliminary work was commenced. Plants of about 55 F_3 families of Mindum x D5 together with the parents and a set of differential hosts were inoculated in November. In December a second set comprising plants of the majority of those F_3 families used in November were inoculated, as a test of the constancy of the types of infection found. By this time it was known that the rust being used was Form 17.

Early in December a second survey of the available rust forms was made. It was found that D5 was quite susceptible to Form 1 to which Mindum was highly resistant. Since these reactions were reciprocal to those given with Form 17, Form 1 was selected for use. One other form, No. 34, looked promising, for, although it was mixed with another form, the indications were that Mindum was susceptible and D5 resistant.

In January the results with Form 17 were obtained. In February, Form 1 was used. By this time Form 34 had been purified and increased. By the middle of April work with Form 34 had been completed.

Accuracy of the Results: Table II gives the results of the preliminary work with Form 17. Only the F_3 families which were tested twice to this form were included in the table. In general, the pure varieties, that is, the parents and differentials, gave more consistent results than the F_3 families. There was a high correlation between the November and December results for 9 of the 12 varieties used; 2 showed medium high correlation and only one fell into the medium low correlation class. Of the 32 F_3 families, 22 appeared in the high correlation classes and 10 showed a low correlation. These figures indicate that there was somewhat more variation in the types of infection on the hybrids than in the types of infection on the varieties, however, the number of tests was rather small. This was to be expected in the case of the heterozygous F_3 families owing to their differences in genetic composition with respect to resistance, but not, however, in the homozygous F_3.

The question then arises as to how many homozygous families there were. Thirteen of the 32 families appeared homozygous susceptible in both tests. No families exhibited complete resistance in both tests. This is not strange inasmuch as D5, the most resistant parent, was only partially resistant. It obviously would have been impossible to have chosen correctly from among the F_3 progeny the families which were homozygous for the amount of resistance possessed by the D5. It is probable that there were several families homozygous for the D5 type of resistance and that some of the apparently homozygous susceptible families were heterozygous. The variability of the reaction obtained when D5 was inoculated with Form 17 may explain the cause

Table II.-- A Comparison of the Types of Infection Produced by Biologic Form 17 on a Series of Mindum x D5 F_3 Families at Two Different Periods.

Variety or F_3 family	Seed Color	Period of development		No apparent infection	Types of infection								Total F_3 plants	Classes of infection*					Correlation of Nov. reading with Dec. reading			
		Time of year	No. days		0	1	2	X-	3	X+	4-	4		R	NR	H	NS	S	High	Medium high	Medium low	Low
Mindum		Nov.	16	6							6	55	67					1	1			
		Dec.	19	6						7	5	4	22					1				
D5		Nov.	16	5					18	2	8		33		1					1		
		Dec.	19	5	3	1			1	6	1		17			1						
Little Club		Nov.	16	4								35	39					1	1			
		Dec.	19									15	15					1				
Marquis		Nov.	16	2								28	30					1	1			
		Dec.	19	2								12	14					1				
Kanred		Nov.	16		6						1	1	8		1				1			
		Dec.	19	8	3				2		1		14		1							
Kota		Nov.	16									13	13					1	1			
		Dec.	19								16		16					1				
Arnautka		Nov.	16									8	8					1	1			
		Dec.	19	2							5		7					1				
Kubanka		Nov.	16	1							3		4					1		1		
		Dec.	19	2					2				6			1						
Acme		Nov.	16							1	5	3	9					1	1			
		Dec.	19	2							8		10					1				
Einkorn		Nov.	16								8		8					1			1	
		Dec.	19	2					10				12	1								
Emmer		Nov.	16		9								9	1					1			
		Dec.	19		11								11	1								
Khapli		Nov.	16		3	7							10	1					1			
		Dec.	19		7	2							9	1								
Total for varieties																			9	2	1	0

(continued)

Table II.-- (Continued, page 2)

Variety or F_3 family	Seed Color	Period of development		No apparent infection	Types of infection								Total F_3 plants	Classes of infection*					Correlation of Nov. reading with Dec. reading			
		Time of year	No. days		0	1	2	X-	3	X+	4-	4		R	NR	H	NS	S	High	Medium high	Medium low	Low
793-1	W	Nov.	16									7	7					1			1	
		Dec.	19					2	3		5	2	12			1						
793-6	W	Nov.	16									7	7					1	1			
		Dec.	19									14	14					1				
793-8	R	Nov.	16						2		3	7	12				1				1	
		Dec.	19						8				8	1								
793-9	R	Nov.	16							4		8	12					1	1			
		Dec.	19								17		17					1				
793-10	W	Nov.	16									7	7					1	1			
		Dec.	19									5	5					1				
793-12	W	Nov.	16									8	8					1	1			
		Dec.	19									12	12					1				
793-13	W	Nov.	16		1			10				1	12		1						1	
		Dec.	19			1		1		1	3	2	8				1					
793-14	R	Nov.	16							3		7	10					1	1			
		Dec.	19									20	20					1				
793-16	W	Nov.	16									13	13					1	1			
		Dec.	19									16	16					1				
793-17	R	Nov.	16						5	4		2	11			1				1		
		Dec.	19						2		4	5	11				1					
793-18	R	Nov.	16			1		10					12	1								
		Dec.	19	1								3	4					1				1
793-19	R	Nov.	16							2		10	12					1	1			
		Dec.	19							12			12					1				

(continued)

Table II.-- (Continued, page 3)

Variety or F_3 family	Seed Color	Period of development		No apparent infection	Types of infection								Total F_3 plants	Classes of infection*					Correlation of Nov. reading with Dec. reading			
		Time of year	No. days		0	1	2	X-	3	X+	4-	4		R	NR	H	NS	S	High	Medium high	Medium low	Low
793-21	R	Nov.	16							6	2	2	10					1		1		
		Dec.	19		1			5		2	2		10			1						
793-22	W	Nov.	16									4	4					1	1			
		Dec.	19								1		1					1				
793-23	W	Nov.	16	2								8	10					1				1
		Dec.	19			1		3	1	1			6		1							
793-27	W	Nov.	16							2		8	10					1	1			
		Dec.	19								1	9	10					1				
793-31	W	Nov.	16									12	12					1	1			
		Dec.	19								4	11	15					1				
794-1	R	Nov.	16							1	2	6	9					1	1			
		Dec.	19									8	8					1				
794-3	R	Nov.	16							1	2	7	10					1		1		
		Dec.	19					5		4			9			1						
794-4	W	Nov.	16							3	3	4	10					1		1		
		Dec.	19			1		1		4	2	4	12				1					
794-5	W	Nov.	16							5	7	1	13					1			1	
		Dec.	19		1	1		11			4	2	19		1							
794-7	R	Nov.	16		1					4	3	1	9				1				1	
		Dec.	19			1		6					7	1								
794-11	R	Nov.	16					2		3	7		12				1				1	
		Dec.	19	2	4	5				5			16		1							
794-13	W	Nov.	16					5	1	6	2		14			1				1		
		Dec.	19	1		1		3	2	8		1	16			1						

(continued)

Table II.-- (Concluded, page 4)

Variety or F_3 family	Seed Color	Period of development		No apparent infection	Types of infection								Total F3 plants	Classes of infection*					Correlation of Nov. reading with Dec. reading			
		Time of year	No. days		0	1	2	X-	3	X+	4-	4		R	NR	H	NS	S	High	Medium high	Medium low	Low
794-15	W	Nov.	16	1				2	4	2	3		12			1				1		
		Dec.	19						1	3	1		5				1					
794-16	W	Nov.	16						4		3	3	10			1				1		
		Dec.	19	3						4	6	7	20					1				
794-17	R	Nov.	16					1	1	1		5	8				1		1			
		Dec.	19						3	3		6	12				1					
795-1	R	Nov.	16						1			5	6				1			1		
		Dec.	19	1								8	9					1				
795-5	R	Nov.	16	1				1	3	2		3	10				1				1	
		Dec.	19								3	9	12					1				
795-7	W	Nov.	16									12	12					1	1			
		Dec.	19									12	12					1				
795-8	W	Nov.	16									8	8					1			1	
		Dec.	19	1	2			5			1	2	11		1							
795-11	W	Nov.	16	5								3	8					1	1			
		Dec.	19							2		10	12					1				
TOTal for F3													1072						14	8	8	2

* R= resistant, NR= near-resistant, H= heterozygous, NS= near-susceptible, S= susceptible.

Note: Only first leaf inoculations were made. There were two sets of plants used, one in November and the other in December.

for the variability of the reaction of the hybrids. If Form 1 or Form 34 had been used the results might have been more consistent than those here reported.

The variations were in some cases quite marked. For example, all of the November set of seedlings of family 793-18 appeared resistant, whereas in December the seedlings, 3 in number, were susceptible. On the other hand, family 794-7 gave near-susceptibility in November but resistance in December. In general, plants inoculated in December appeared more resistant than those inoculated in November. This can be attributed principally to environmental effect for it is well known that there is a weaker development of rust during the short frequently cloudy days of mid-winter than when the days are bright and longer (Stakman, E.C. and Levine, M.N., 1919).

In estimating the accuracy of the types of infection that appeared on the hybrids the behavior of the rust on pure varieties may be taken as a criterion of the average amount of variation that occurred. The November results for Mindum show that about 90 per cent of the plants had 4 type infections and about 10 per cent had the 4- type. The December results for this variety show only 25 per cent of the plants with 4 type infection, the remaining 75 per cent having X+ and 4- types. In November the 4- type of infection was produced on 30 per cent of the D5 plants and the 3 type on 64 per cent. Yet, in December, the 3 and 4- types of infection appeared on only 2 out of a total of 17 plants which were infected, the remainder of the plants having 0, 1, and X- types of infection.

Similar, although less striking, results were obtained with Kota, Arnautka, Kubanka, Acme, Einkorn, and Khapli. In all cases there was weaker rust development in December, and therefore more apparent resistance of the plants, than in November. Consequently, although it has been necessary to establish a dividing line between the 0, 1, 2, X-, and 3 infection types on the one hand and the X+, 4- and 4 types on the other for the purpose of tabulating and interpreting the data, it must be remembered that reaction results not only varied <u>among</u> the susceptible or the resistant types of infection but that they fluctuated to some extent <u>between</u> certain resistant and susceptible types.

Levine, in recent investigations*, states that environmental conditions may cause fluctuations in the virulence of the rust, that is to say, in the extent of its development on a host. He found that, although inoculations of a given host with a certain form might produce type 0 or type 1 infections, similar inoculations at another time might result in type 1 or type 2 infections. However, it was found that when type 0, 1, or 2 infections were produced at one time as a result of a certain inoculation, a similar inoculation never resulted in 3 or 4 type infections. Likewise reactions that produced a type 4 infection at one time resulted sometimes in type 3 infections but neither the 3 or 4 types ever appeared as 0, 1, or 2 types under favorable conditions of light, heat, etc. The fluctuations in rust development were small. Other recent work† indicates that a considerable degree of variability is sometimes obtained even when conditions seemed rather favorable.

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* Unpublished results.

† Unpublished data by Hayes and Aamodt.

There are several possible explanations for the occurrence of deviations in types of infection on homozygous varieties. The state of health of the plant may have been an influencing factor. P. graminis is an obligate parasite that flourishes best on healthy growing wheat plants. If for any reason, such as injury, disease, or lack of water, the plant becomes sickly the rust may develop somewhat differently than it otherwise would. This was noticeable in the work with Form 17 and with the other two forms. Yet it was not thought adviseable in taking data to make any allowances, inasmuch as the infection types may have been, in most cases, quite normal. Either the plants were discarded or the types of infection were recorded just as they appeared. Only badly injured plants, or those which were dead or dying from the effects of root and foot rots,were thrown out. In recording the data consideration was always taken of the reactions of the plants in the pots of Mindum and D5 checks.

Another possible reason for the occurrence of these deviations may have been the uneven distribution of light to the leaves of the seedlings that were tested. Owing to very limited greenhouse space, at the time Form 17 and Form 1 were used, the pots had to be placed so close together that there was frequently not more than an inch of distance between one pot and the next. Many of the first leaves of the hybrid seedlings as well as of the parents and several of the differential varieties hung down between the pots during the period of rust development and were thereby subjected to a considerable amount of shade while other leaves were receiving direct sunlight. The pots were changed around occasionally but this did not greatly affect the habit of some leaves to hang down and others to remain fairly erect. Since the vigor of a plant depends largely on the amount of photosynthesis carried on in its leaves and since the development of rust is dependent at least partially on the vigor of the plant and on the amount of sunlight received it is clear that here was a probable source of deviation.

Deviations may also have been produced as a result of varying weather conditions, as has been discussed. The effects of temperature, of different humidity conditions during incubation and of the time and amount of watering with respect to sunlight, all may have played a part in producing variations of infection types, despite the fact that an attempt was made to treat all the pots alike from the time of planting the seed until the data were taken. But regardless of the uniformity of treatment given to the various F_3 families there is one other possible source of variation - a difference in the parasitic capabilities of the urediniospores belonging to a single biologic form.

From the foregoing discussion it should not be concluded that the variations were so great as to obscure the results. The reaction of the F_3 plants to the different forms of rust was constant within certain limits and the fact that the plants which were tested were of the third hybrid generation allowing them to be considered as families each arising from a single F_2 plant makes the interpretation of the various reactions a fairly definite matter. But owing to the unavoidable variations that must have occurred it would be erroneous to state with an air of finality the exact class in which some families of a doubtful degree of resistance or susceptibility should be placed. Families which were classed as either resistant or susceptible to biologic Forms 34 and 1 are believed to be accurately classified, as little variation in the type of reaction of the parents was obtained with these forms.

The data in Table II show Kanred with some type 3 and type 4 infections in addition to the 0 type and a number of leaves with no infection apparent. Kanred is resistant to Form 17 giving normally some 0 type infections with the remainder of the plants showing no signs whatever of infection. The appearance of pustules on occasional plants in pots of Kanred indicated either that the seed was mixed or that the rust form was not pure. When additional pots of Kanred were inoculated with rust from pustules on the plants having 3 or 4 type infections all of the plants were resistant excepting one or two per pot, which produced rust pustules. This clearly proved that such plants were not pure Kanred. Similarly it has been found for other varieties that plants producing unexpected types of infection were not from pure seed of the variety used.

Photographic Methods: Much attention was given to the obtaining of photographs of leaves showing the reaction of the parents and hybrids to each of the three biologic forms. Photographs are of value both as illustrations of the types of infection that appear and as permanent records of the results obtained. The method used for preparing material for the camera was to cut off the end portions of affected leaves to the length of 1½ inches and paste them immediately on white cardboard. The picture was then taken natural size before the leaves had a chance to shrink. In selecting material for photographing an endeavour was made to choose F_3 families or pots of parent plants that were truly representative.

EXPERIMENTAL RESULTS.

The Seed Color Ratio in F_3: Of 329 F_2 plants classified 247 were red-seeded and 82 white-seeded, making a 3:1 ratio for seed color. (See Table III). There was sufficient seed of 109 of the F_2 plants to test the mode of reaction for three forms of rust. Of the remaining white-seeded F_2 plants, 28 had only enough seed for two forms and 192 were either red-seeded or too low in number of seed to be of use.

Table III.-- Classification of Mindum x D_5 F_3 Families on the Basis of Seed Color.

No. of F_2 family	F_3 families	
	Red seed	White seed
793	21	10
794	12	5
795	10	3
796	10	1
797	4	1
798	11	4
799	20	3
800	5	1
801	4	3
802	11	4
803	34	13
804	18	0
805	17	8
806	23	9
807	18	3
808	9	1
809	15	8
810	5	5
	247	82
	3	1

It was thought adviseable to test F_3 progeny of only those red-seeded F_2 plants having sufficient seed for three forms of rust, owing to there having been three times as many red-seeded plants as white-seeded. In addition to the foregoing, seed of 46 white-seeded F_2 plants grown in another part of the nursery was used. The F_3 of 36 F_2 plants was tested to three rust forms but the other 10 F_2 plants had only enough seed for two tests. In running the greenhouse work the F_3 seedlings were inoculated in sets of from 25 to 50 families, there being one F_3 family per pot. F_3 families from white-seeded F_2 plants with sufficient seed for three rust forms were included with F_3 families from red-seeded F_2 plants whereas the remaining progeny of white-seeded F_2 parents were worked with separately.

Results of Inoculations With Form 17: The experimental data for Form 17 are given in Table IV (See Appendix). A total of 40 pots of Mindum and D5 were inoculated as controls, there being several pots of each for every set of F_3 families used.

A complete set of differential varieties was inoculated with the first lot of hybrids and another set at the conclusion of the work with this form. Altogether, 174 F_3 families were tested. Of these, 85 were from red-seeded parents and 89 from white-seeded parents. A total of 2168 F_3 plants were inoculated; of these, 1906 or 88 per cent showed various types of infection.

The types of infection on Mindum ranged from X- to 4. There were 4- or 4 types of infection, indicating susceptibility, on 133 out of 136 plants. The 3 remaining plants appeared in two different pots. The appearance of X- and 3 types of infection on these three plants might be accounted for in two ways. First, they could have been due to deviations such as are described in the preliminary work of this paper. Second, the plants may not have been true Mindum owing to mechanical mixture of seed or to natural crossing in the field. Natural crossing in wheat occurs in many wheat growing regions (See summary by Hayes and Garber, 1921). Hayes (1919) found that 2 to 3 per cent of natural crossing occurs at the Minnesota station.

The types of infection on D5 ranged from 0 to 4, each type being represented. Of 103 infected plants only 41 appeared resistant whereas 62 appeared susceptible. There were only 3 pots in which every plant seemed resistant; these were all inoculated at the same time. On the other hand there was only one pot with all plants susceptible. Why there should be such a wide range in types of infection on a presumable pure variety of wheat is rather unexplainable.

The reactions of the first set of differentials were entirely according to expectation. The second set gave consistent reactions, although the rust development was somewhat weaker, probably due to unfavorable weather conditions.

In Table V the results obtained with Form 17 are summarized for the F_3 progeny of red-seeded and the white-seeded F_2 plants, respectively. The classes of infection used are the same as those described for the preliminary work with Form 17. The distribution of the F_3 families of red-seeded parents was very similar to that of the progeny of white-seeded parents. There is no evidence of a correlation of red seed color with resistance, in fact, the number of near-resistant F_3 families of white-seeded F_2 plants exceeded that of the progeny of red-seeded F_2 plants and the

Table V.-- The Reaction of the F_3 of Mindum x D5 to Three Biologic Forms of Puccinia graminis tritici.

Parents or F_3 families	Biologic form used	Classes of infection					Total parent pots or F_3 families
		R	NR	H	NS	S	
Mindum.........	17				2	18	20
D5	17	3	4	5	7	1	20
Red-seeded F_3	17	1	8	19	26	31	85
White-seeded F_3	17		12	24	22	31	89
Totals for F_3		1	20	43	48	62	174
Mindum.........	1	20	3				23
D5	1		4	2	11	6	23
Red-seeded F_3	1	27	42	6	6	4	85
White-seeded F_3	1	23	43	5	14	4	89
Totals for F_3		50	85	11	20	8	174
Mindum.........	34				5	26	31
D5	34	27	6				33
Red-seeded F_3	34	18	22	18	12	15	85
White-seeded F_3	34	6	13	9	5	1	34
Totals for F_3		24	35	27	17	16	119

number of near-susceptible F_3 families from white-seeded parents was less than that of the progeny of red-seeded F_2 plants. A graphic demonstration of the close similarity of the results is shown in Figure 1.

Combining the results for red-seeded and white-seeded F_2 plants gives 1 resistant F_3 family, 20 near-resistant, 43 heterozygous, 48 near-susceptible, and 62 susceptible. A total of 63 families appeared to be homozygous and 111 exhibited various degrees of heterozygosity. The preponderance of susceptible types is quite in accordance with expectation considering the parental reactions.

Curves Plotted from the Results Given in Table 5 for the Red-seeded and White-seeded F_3 Families.

FIGURE 1.

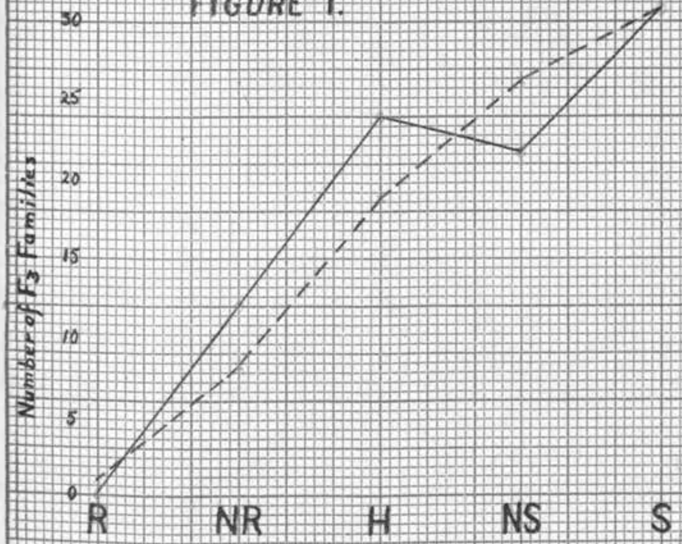


FIGURE 3.

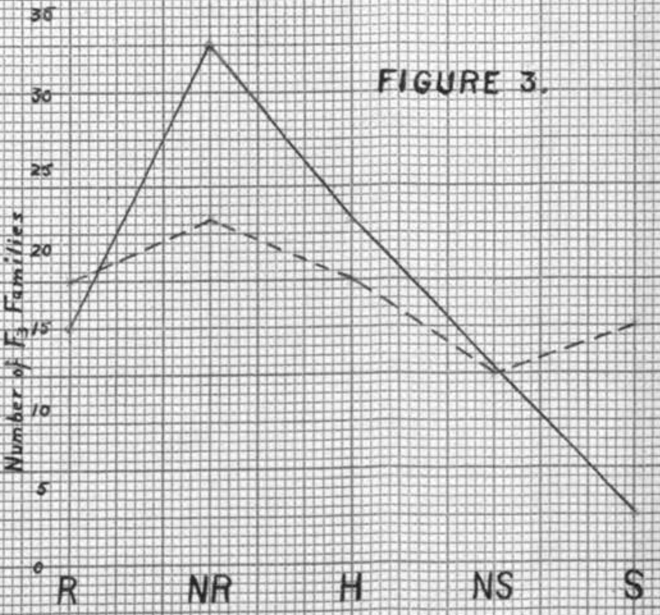
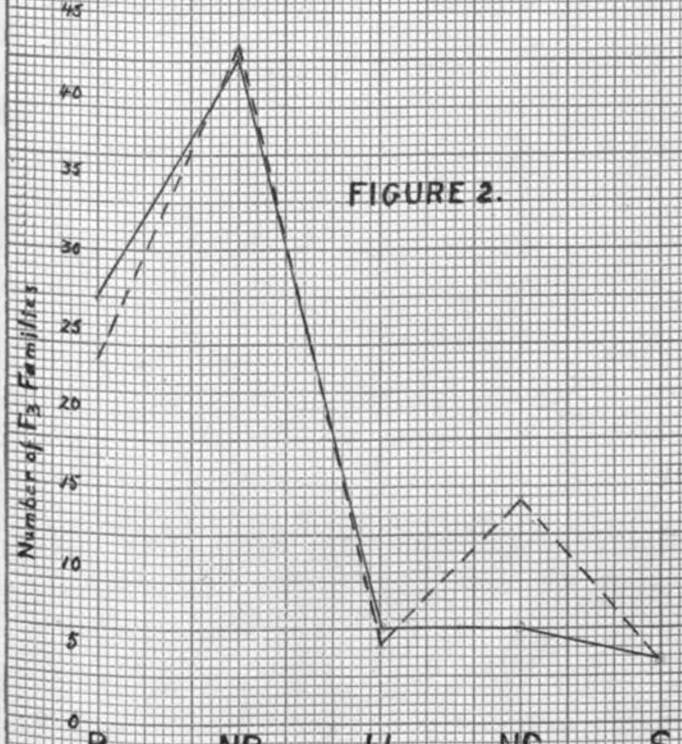


FIGURE 2.

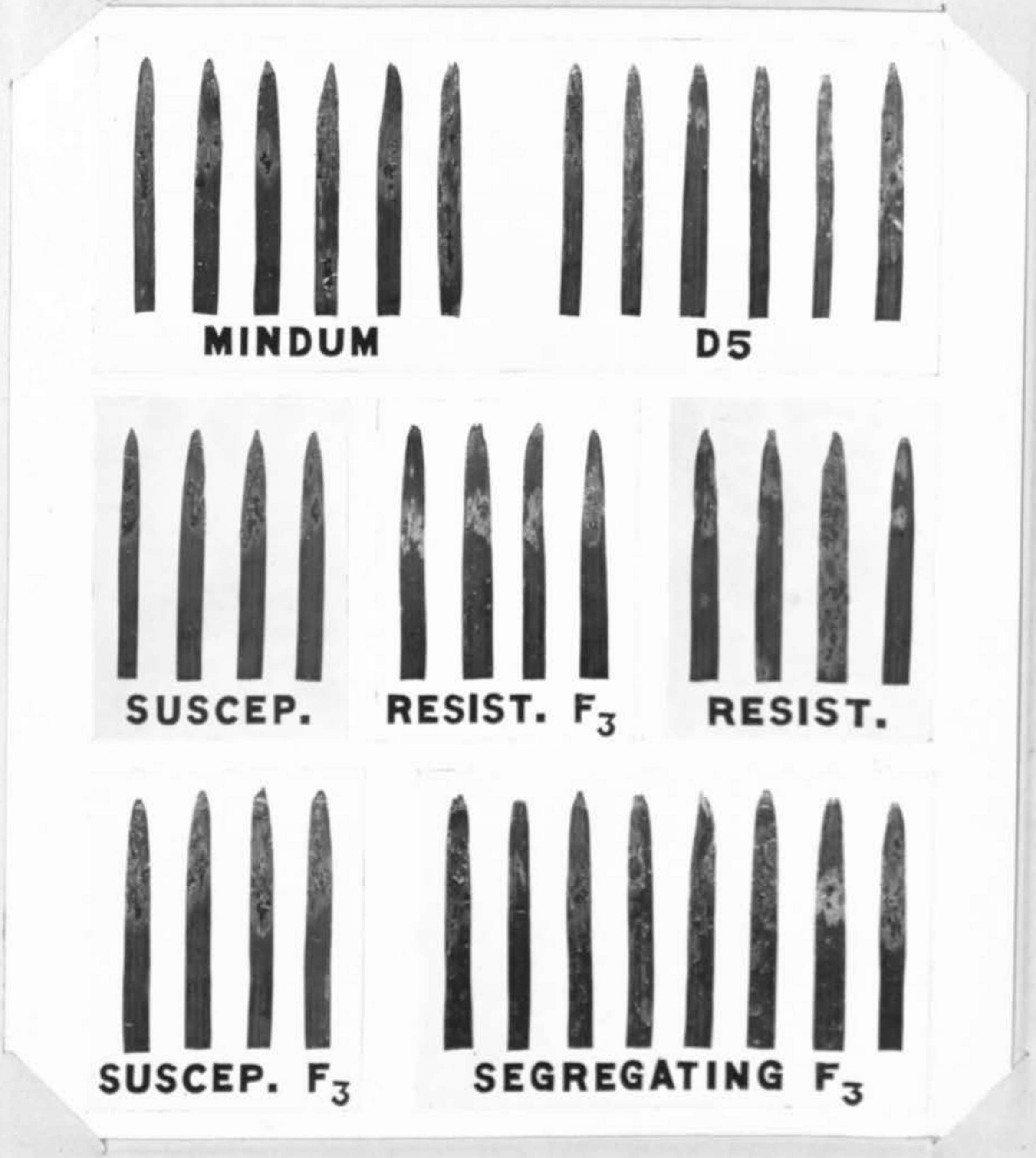


——————— Red-seeded
- - - - - - - White-seeded

R = Resistant
NR = Near-resistant
H = Heterozygous
NS = Near-susceptible
S = Susceptible

Figure 1 illustrates the reaction to Form 17
Figure 2 illustrates the reaction to Form 1
Figure 3 illustrates the reaction to Form 34

PLATE I.



The reaction of Mindum, D5, and F_3 hybrids to Biologic Form 17. Mindum is susceptible and D5 is resistant. The F_3 families shown are, central figures, left to right: 799-1, susceptible; 808-1, resistant, 798-1, resistant; lower figures: 809-23, susceptible; 803-37, heterozygous.

Considering the results in relation to the parent varieties it may be noted that Mindum was consistently susceptible or near-susceptible, and that only a small percentage of the pots of D5 plants proved susceptible. On this basis the greater part of the susceptible hybrid families may be considered to have the Mindum type of inheritance for rust reaction. Therefore a single main differential factor fairly satisfactorily explains the results. The variable results obtained with the D5 parent preclude closer analysis.

Results of Inoculations with Biologic Form 1. The data obtained with Form 1 are given in full in Table IV and summarized in Table V. A total of 174 F_3 families were tested. Of these, 85 were from red-seeded F_2 plants and 89 from white-seeded F_2 plants. The number of F_3 plants inoculated was 3222; of these, 3154, or 98 per cent, showed infection.

The reaction of the parent varieties, Mindum and D5, to Form 1 is the reciprocal of that with Form 17. A total of 284 plants of Mindum, in 23 pots, and 194 plants of D5, also in 23 pots, were inoculated. Of the 243 Mindum plants that were infected, 197 showed the 0 type of infection with a killing of the leaf tips and 5 had a 4 type infection. One of the latter 5 seedlings had a single large pustule on the first leaf near the sheath. The tip of the leaf showed the typical killing of the other plants. A pot of Mindum plants was inoculated with spores from this pustule and a 4 type infection was produced on every leaf thereby indicating that the original pustule probably arose from a chance spore of some other form, presumably from Form 17, which was in another part of the same section of the greenhouse.

Three of the four other seedlings were in a single pot. It is quite probable that these results were due to accidental infection. A single chance spore may have produced a large pustule on one of the plants used for increasing Form 1 and the rust inoculum from this pustule may have been transferred to the three seedlings in question at the time of inoculation. Accidental infection of this nature is almost unavoidable, where many rust forms are being worked with; fortunately it is of comparatively rare occurrence.

Somewhat as with Form 17, the type of infection on D5 ranged from 0 to 4. Of 194 D5 plants, 70 appeared resistant and 97 susceptible. In no D5 pots were all of the plants resistant but in 4 the majority of them were resistant. These pots were classed as near-resistant, 2 others as heterozygous, 11 near-susceptible, and 6 susceptible.

The reactions of the first set of differentials were not as consistent as was found with Form 17. Not only was there, in general, a weaker development of rust on this set than on the second set but there was considerably more deviation within several of the varieties, especially Kubanka, Acme and Arnautka.

The distribution of families planted from red seed was similar to that of the progeny of white-seeded plants. A lack of correlation of seed color with resistance or susceptibility is manifest. (See Plate II).

Combining the results for the progeny of red-seeded and white-seeded F_2 plants gave 50 resistant F_3 families, 85 near-resistant, 11 heterozygous, 20 near-susceptible, and 8 susceptible. There was a much larger proportion of resistant and near-resistant families than of susceptible and near-susceptible. This was to be

PLATE II.

The reaction of Mindum, D5, and F_3 hybrids to Biologic Form I. Mindum is resistant and D5 is susceptible. The F_3 families shown are: 802-6, heterozygous; 809-5, resistant; 804-17, susceptible.

expected from progeny of parents one of which was wholly resistant and the other, which under the conditions of the experiment, gave somewhat variable results. The total number of apparently homozygous families was 38 and of the heterozygous families 81. Resistance is apparently dominant.

Considering the results for Form 1 in relation to the reactions of the parent varieties brings out the fact that Mindum was consistently resistant or near-resistant, whereas resistant plants only appeared in a small proportion of D5 pots and in no case was every plant in a pot resistant. Approximately one-eighth of the pots of Mindum were near-resistant and seven-eighths were resistant. On this basis, 58 of the 174 F_3 families had the Mindum type of resistance. As with Form 17, a single differential factor fairly satisfactorily explains the results. The variable results obtained with the D5 parent prevent a more detailed analysis.

Results of Inoculations with Biologic Form 34. Table IV contains the detailed results obtained with Form 34. Of 119 F_3 families tested, 85 were the progeny of red-seeded F_2 plants and 34 were the progeny of white-seeded F_2 plants. A total of 2680 F_3 plants were inoculated and of this number 2630, or over 98 per cent, showed infection. Unlike the reactions to the two previous forms, the ranges of the types of infections for the parents are here quite distinct. Mindum gave 26 pots entirely susceptible and 5 near-susceptible, the range of infection being from X- to 4. Of the 375 Mindum plants showing infection, only 9 were outside of the susceptible class. These were in the semi-resistant class, 4 having the X- type of infection and 5 having the 3 type.

Classifying the pots of D5 plants on the same basis as F_3 families, 27 were resistant and 6 were near-resistant. Infection appeared on 327 of the inoculated plants. Of these, 9 reacted with X+ infections and 1 gave a 4 type. These unexpected reactions may be explained as due to impure seed or to accidental infection. The reactions of Mindum and D5 to Form 34 were therefore somewhat similar to those obtained with Form 17 but much more differential. They were reciprocal to the results secured with Form 1.

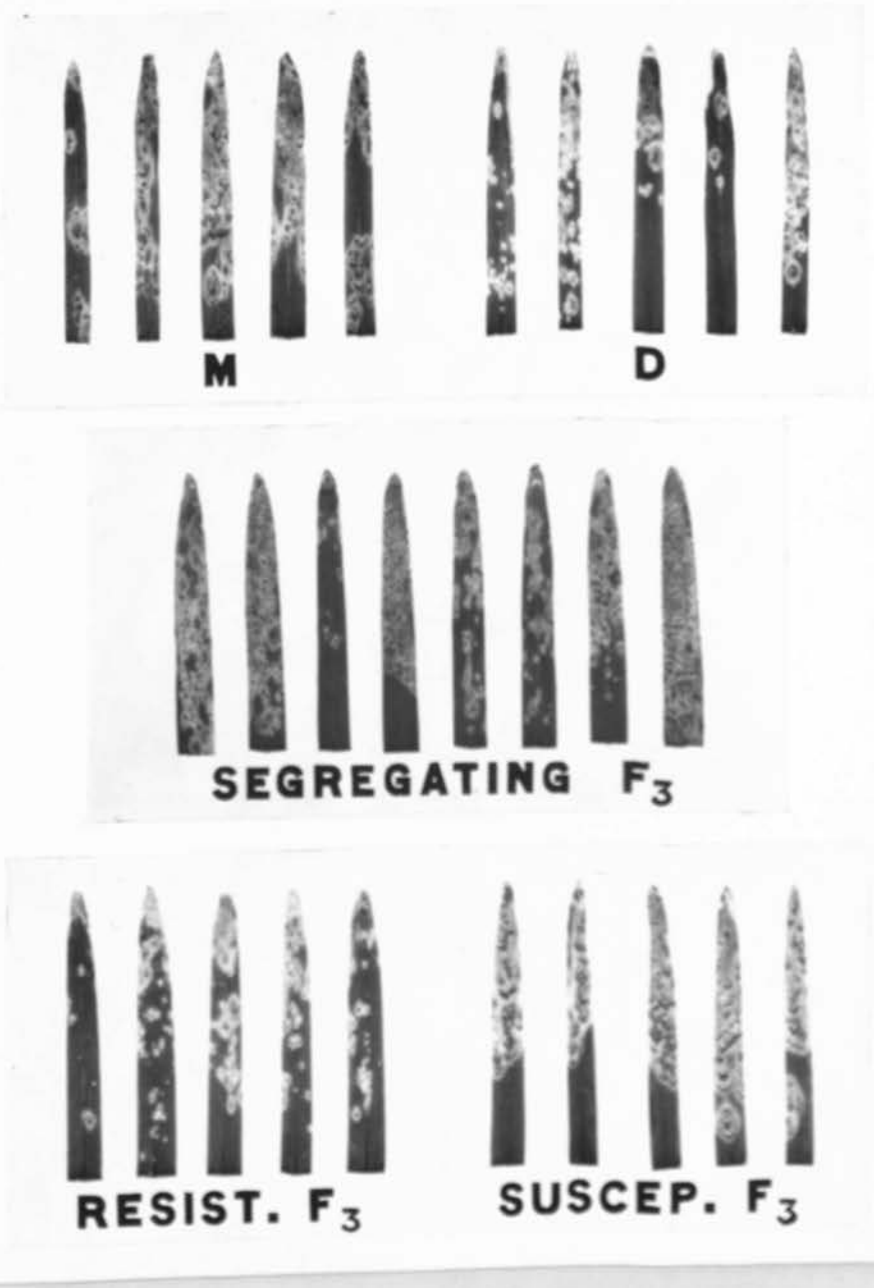
It was noticeable that Form 34 produced in general a greater amount of hypersensitiveness on both parent and hybrid plants than either Form 1 or Form 17. These sharp hypersensitive areas occurred around a large proportion of the pustules of types 3, 4-, and 4 infections. Usually 4- and 4 types show chlorosis but practically no necrosis. Here, however, about 50 per cent of the type 4 pustules showed such a decided necrotic bordering that the advisability of creating a special class for this type of infection was considered. Eventually it was concluded that the establishment of an additional type would possibly lead to some confusion without really proving of value, since it was apparent that, plants infected in this manner were susceptible, on account of the development of numerous large pustules.

Only one set of differentials was inoculated owing to the fact that all the F_3 and parent pots were inoculated within the space of one week. Two pots of each differential variety were used. The reactions of half of the varieties showed fully as much variation as was found with Form 1. The relatively large number of X- and X+ types of infection that appeared was probably due to the tendency of Form 34 to produce hypersensitive areas. The distribution of progeny of the red-seeded F_2 plants in the various classes of infection approached that of the progeny of the white-seeded plants. The two fairly large deviations that did occur were in opposite directions and therefore not significant. (See Plate III).

To summarize the data concerning the mode of inheritance of rust resistance with respect to seed color, it may be stated that no correlation was found to exist between the two.

Considering the combined results for Form 34, as summarized in Table V, 24 F_3 families were homozygous for resistance, 35 were near-resistant, 27 heterozygous, 17 near-susceptible, and 16 homozygous for susceptibility. The total number of apparently resistant families was 40. When the results for Form 34 are considered with respect to the reactions of the parent varieties it is seen that Mindum was consistently either susceptible or near-susceptible, whereas D5 was resistant or near-resistant. Between three-fourths and four-fifths of the pots of D5 were resistant and the remainder were near-resistant. On this basis between 29 and 30 of the F_3 families were as resistant as D5. The proportion of 89.5 (119-29.5) : 29.5 is an excellent 3:1 ratio indicating the presence of a single differential factor. Resistance was apparently dominant.

PLATE III.



The reaction of Mindum, D5 and F_3 hybrids to Biologic Form 34. Mindum is susceptible and D5 is resistant. The F_3 families shown are: 807-18, heterozygous; 805-1, resistant; 804-17, susceptible.

Table VI.-- The Reaction of the F_3 Families to Biologic Forms 1 and 34.

		Reaction to Form 1					
		R	NR	H	NS	S	
Reaction to Form 34	R	7	11	2	3	1	24
	NR	12	15	4	4		35
	H	5	18		4		27
	NS	5	9	1	2		17
	S	5	6	1	1	3	16
		34	59	8	14	4	119

Table VII.-- The Reaction of the F_3 Families to Biologic Forms 17 and 1.

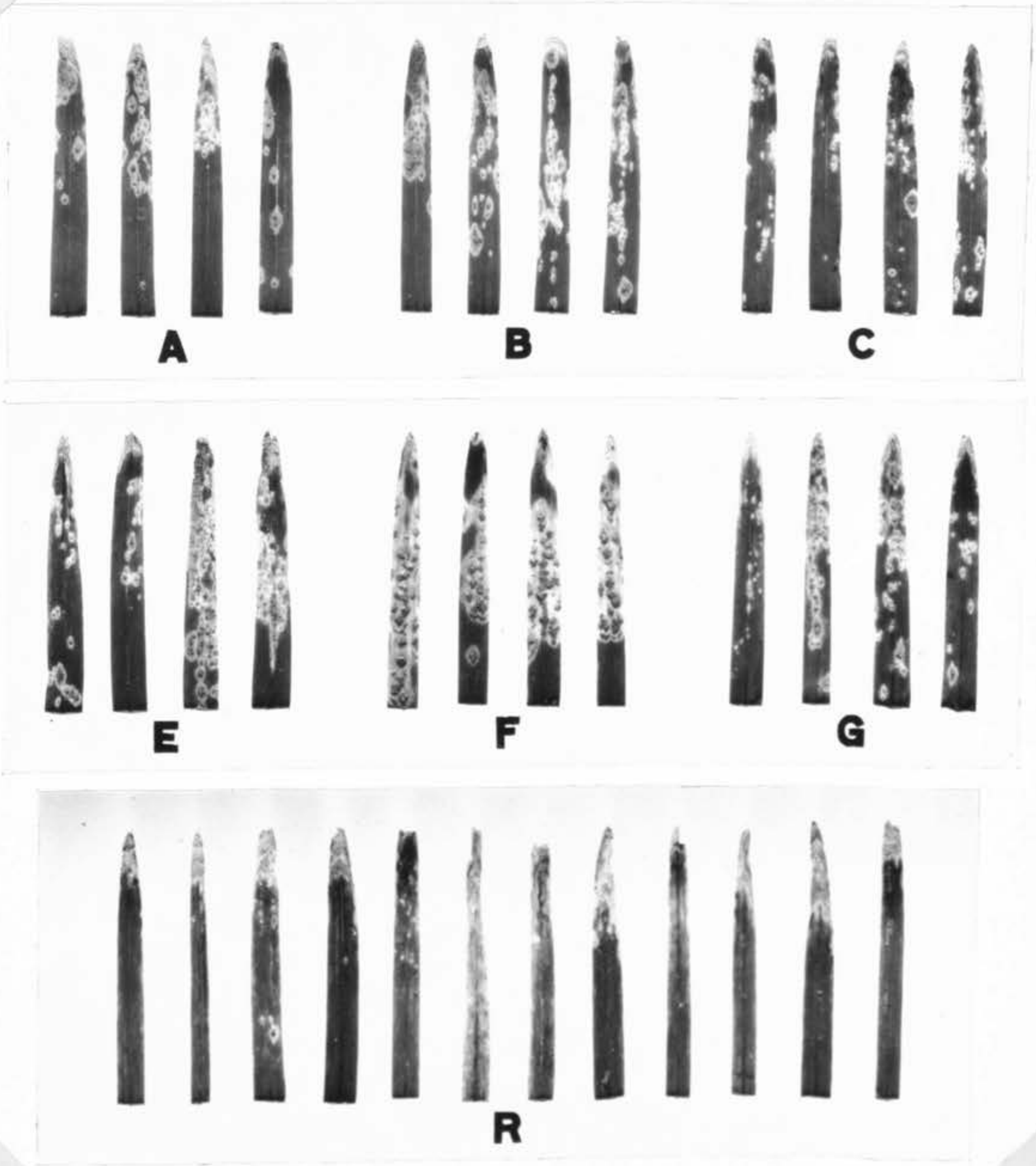
		Reaction to Form 17					
		R	NR	H	NS	S	
Reaction to Form 1	R		3	9	14	24	50
	NR		8	22	26	29	85
	H		3	3	3	2	11
	NS	1	5	7	5	2	20
	S		1	2		5	8
		1	20	43	48	62	174

Combinations of Susceptibility and Resistance of F_3 Families to Form 1 and Form 34: Table VI correlates the summarized data for Form 1 and Form 34. All combinations of susceptibility and resistance to the two biologic forms appeared. Seven F_3 families were definitely resistant to both forms, as, for example, 809-21 and 805-16 (See Table IV and Plate IV, C and B) Four families were quite susceptible to both forms, as 804-7 and 804-17 (See Plate IV F and Plate III). Other families were resistant to one form and susceptible to the other, as 809-6 which was resistant to Form 1 and susceptible to Form 34 (See Plate IV H) and 809-8 which reacted reciprocally to 809-6 (See Plate IV G). Other F_3 families were resistant or susceptible to one form and intermediate to the other, as 806-24 (Plate IV E), 805-4, 802-6 and 799-21. Still other families were heterozygous to both forms, as 799-4 and 799-9.

The most significant feature of Table VI is that 7 F_3 hybrid families are shown to have been definitely resistant to both biologic Form 1 and 34. Considering the reaction of the parent varieties to these biologic forms it is very likely that a few of the near-resistant families were likewise homozygous in their reaction. On this basis it would seem that 2 main differential factors may explain the results obtained. These factors are inherited independently which makes possible the combining of resistance to both forms in a single variety.

Combinations of Susceptibility and Resistance of F_3 Families to Form 17 with Form 1 and Form 34: There is not much value in studying the correlation of the F_3 reactions to Forms 17 and 1 since, as was explained previously, the parents did not

PLATE IV.



The reaction to Biologic Form 34 of F_3 families having various combinations of resistance, susceptibility, and heterozygosity to Biologic Forms 17, 1 and 34. A, B, and C are F_3 families from white-seeded F_2 plants. The mode of reaction of these F_3 families to all three biologic forms is given in the following:

F_3 family	Index letter	Reaction to biologic form		
		17	1	34
807-10	A	H	H	R
805-16	B	S	R	R
809-21	C	S	R	R
806-24	E	S	H	R
804-7	F	S	S	S
809-8	G	R	S	R
796-4	R	R	R	R

give a well defined reciprocal reaction to either biologic form. Table VI shows that 5 families were susceptible but none resistant to both forms.

Table VIII summarized the combined results for Form 17 and Form 34. No F_3 families proved resistant to both forms but there were 6 families susceptible to both forms. Various combinations of resistance and susceptibility occurred.

Combinations of Susceptibility and Resistance of F_3 Families to Forms 17, 1 and 34: All possible combinations of resistant and susceptible and heterozygous reactions to the three biologic forms appeared in the F_3 families, with the exception of combinations involving complete resistance to Form 17. Examples of some of the combinations are: 809-8 (See Plate IV G), reproducing the reactions of D5; 803-28, giving the Mindum type of reaction; 796-4 (See Plate IV R) with near-resistance to Form 17 and resistance to Forms 1 and 34; 804-7 (See Plate IV F) showing high susceptibility to the three forms; 799-4, heterozygous to the three forms; 807-10 (See Plate IV), heterozygous to Forms 17 and 1 and resistant to Form 34; etc.

The Reaction of the F_3 Families from White-Seeded Parents to Form 1 and Form 34: Table IX correlates the results obtained for the F_3 families from white-seeded parents with Forms 1 and 34. Out of a total of 34 families, 12 approached resistance to both forms and 2 of these were wholly resistant to the two forms. The indications of 3:1 ratios for Form 1 and 34 are here substantiated in an unusually close 15:1 ratio.

The object of giving special treatment to the F_3 progeny of white-seeded F_2 plants is a recognition of the fact that the

Table VIII.-- The Reaction of the F_3 Families to Biologic Forms 34 and 17.

		Reaction to Form 34					
		R	NR	H	NS	S	
Reaction to Form 17	R			1			1
	NR	5	2	2	2	1	12
	H	4	9	8	5	6	32
	NS	6	11	8	5	3	33
	S	9	13	8	5	6	41
		24	35	27	17	16	119

Table IX.-- The Reaction of the Progeny of White-seeded F_2 Plants to Biologic Forms 1 and 34.

		Reaction to Form 1					
		R	NR	H	NS	S	
Reaction to Form 34	R	2	2	1		1	6
	NR	3	5		1	4	13
	H	1	7			1	9
	NS		2	1	1	1	5
	S		1				1
		6	17	2	2	7	34

economic aspects of a problem warrant careful consideration. D5, although high in rust resistance is a poor milling wheat. Owing to the difficulty of distinguishing the threshed grain of one red durum from another, millers have come to discriminate against all red durums. There is consequently no immediate future for a new rust resistant red durum, even though it be of good milling quality

CONCLUSION.

The study of the reaction of the F_3 generation of a cross between Mindum and D5, two durum wheats, to three biologic forms of <u>Puccinia graminis</u> has shown that all combinations of susceptibility and resistance to these forms may appear. Owing to the reactions of Mindum and D5 to Form 17 not being clearly differentiated a definite factor analysis of the reaction of the F_3 families was not possible. There was indicated, however, the presence of a single factor. With Form 1 the results can be explained on the basis of a single main factor difference. The character of the two parental reactions to Form 34 differed from that for the two preceding forms in that the respective ranges for Mindum and D5 were very narrow and quite distinct from each other. The data for this form can be satisfactorily explained on the basis of a single factor difference with respect to resistance and susceptibility.

No evidence of a correlation between seed color and resistance and susceptibility to rust was found.

Since the action of each biologic form was, in general, quite uniform on individual plants of the differential varieties and also on the Mindum, D5 and F_3 plants, barring the X- and X+

types of infection, it may be concluded that the urediniospores of each form probably were of the same genetic sonstitution. Therefore the factors concerned with susceptibility and resistance must have been located in the plants themselves. Furthermore, since biologic forms differ in their parasitic capabilities on the same varieties of wheat, there genetic constitution cannot be the same.

It is probable, then, that factors governing susceptibility and resistance to different biologic forms used in this experiment are different in nature and are located in different chromosome pairs. The various combinations of resistance and susceptibility to three biologic forms that appeared in F_3 families in this study admit of no other explanation.

The results described in this paper for Form 1 and Form 34 show that, when two varieties of wheat acted reciprocally with respect to resistance and susceptibility to two biologic forms, several of the F_3 families resulting from crossing the two varieties proved to be resistant to both biologic forms. Further, one of the F_3 families resistant to Form 1 and Form 34 was near-resistant (or resistant as D5) to Form 17 as well. These results furnish grounds for the belief that eventually a variety can be produced which is resistant to all biologic forms.

SUMMARY.

1. A study was made of the parasitic capabilities of three biologic forms of <u>Puccinia graminis tritici</u> on the F_3 generation lines from a cross between two varieties of <u>Triticum durum</u>.

2. The parental varieties, Mindum and D5, reacted reciprocally to two of the biologic forms used.

3. The constancy of the parasitic capabilities of the biologic forms had been determined previously and as additional evidence complete sets of differential varieties were inoculated at the commencement and at the completion of the work with each form. Form 17 attacked Mindum heavily but developed less strongly on D5. Form 1 produced no uredinia on Mindum but developed vigorously on D5. On the other hand, Form 34 attacked Mindum severely but developed weakly on D5.

4. A separate set of 10 to 20 plants from each F_3 family was grown for use with each form of rust. Only first leaves were inoculated.

5. All gradations between complete susceptibility and resistance to the three forms of rust appeared in the F_3 families (excepting for complete resistance to Form 17).

6. The results with Form 17 were somewhat doubtful due to the variation in types of infection of the D5 parent. The presence of a single factor seemed probable.

7. A single main factor difference explained the results obtained with Form 1.

8. A single pair of genetic factors satisfactorily explained the manner of reaction to Form 34.

9. No relation was found between seed color and rust resistance.

10. All combinations of susceptibility and resistance of individual F_3 families to Form 1 and Form 34 appeared. Out of a total of 119 F_3 families, 7 were highly resistant to both forms

of rust. Two of these 7 families were white-seeded. Of the 5 families from red-seeded F_2 plants, one was also as resistant as the resistant parent to Form 17. Varieties resistant to more than two biologic forms of rust may therefore be produced by hybridization.

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APPENDIX

Table IV.-- The Reaction of F_3 Plants of the Cross Mindum x D5 to Three Biologic Forms of Puccinia Graminis Tritici.

Parents, differentials, of F_3 families	Seed color	Results for biologic form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
Mindum	W	15									24	24	17	1	19	8							28	17	23				4	5	31	27	112	202
D5	R	15		1			1		10	3		15	17	4	4	3		10	1	2			24	17	22	34	98		23	3	2		1	183
Little Club		15	2								9	11	17									24	24	16									25	25
Marquis		15									7	12	17								8	4	12	16									21	21
Kanred		15	14									14	17	14									14	16	2								18	20
Kota		15	1								9	10	17						14				14	16	1				2	3		4	16	26
Arnautka		15	7								7	14	17		11			1			3		15	16							1		22	23
Kubanka		15	2								9	11	17	2	3				6		1	1	13	16							3		18	21
Acme		15									9	9	17	2					11		1	1	15	16									21	21
Einkorn		15	3					9				12	17						14				14	16	2				9	12				23
Emmer		15	1	9								10	17	1	12								13	16	1	1	19		2					23
Khapli		15	2		7							11	17			13							13	16			20							20
793-1	R	16									7	7	17		8				1		1		10	17					4	1	2			7
-12	R	16									8	8	17		13							2	15											
-13	R	16			1		10				1	12	17	1	13						3		17											
794-13	R	16					5	1	6	2		14	17		2						2	6	10											
-16	R	16						4		3	3	10	17	1				1	4		4	5	15											
795-8	R	16									8	8	17	1	8						1		10											
796-1	W	15							5		6	11	17	1	5						1	9	16	17		5	10		5		1			21
-3	R	15	1								9	10	17		15								15	17		6	9		1					16
-4	R	15		1					7		2	10	17	1	13								14	17		9	2		3					14
-5	R	15							3		8	11	17	2	11								13	17		1	4	1	9		4			20
-6	R	15					7		4			11	17	1	9				1		1		12	17		1	1		10		5		1	18
-7	R	15							3		10	13	17		9				2		2		13	17	1	3	8		1					13

(continued)

Table IV.-- (Continued, page 2)

Parents, differentials, or F_3 families	Seed color	Results for biologic form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
796-8	R	15							3		7	10	17	2	9								11	17	1				4		7		2	14
-10	R	15	1						1		11	13	17		7			1	3	1	2	2	16	17	1	9	6			3				19
-11	R	15							1		7	8	17	1	15								16	17		1	2		5		1			9
797-1	R	15							5		2	7	17		9	1					2		12	17			2		4	8	3	3	1	21
-2	W	15						2	3		7	12	17	2	6	1							9	17			3		12	2	4			21
-5	R	15									12	12	17		12				1		2		15	17	2				11		2			15
798-1	R	15		1			1		6			8	17		10				1		1	1	13	17		1	5		9					15
-2	R	15							2		8	10	17	2	10				2				14	17	3	4	2		5					14
-3	W	16									10	10	16						8		2		10											
-6	R	15									13	13	17		11								11	17	5	1	1			1	3	3	1	15
-9	R	15						1			14	15	17	1	11			2			1		15	17	5		1		2	5	4		1	18
-12	R	15									14	14	17	1	14								15	17			15		5					20
-17	W	15	2							1	8	11	16		17								17											
799-1	R	15									14	14	17	1	10				1				12	17					4		8		2	14
-4	R	15							3	1	9	13	17		6						1	5	12	17				2	8		5			15
-5	R	15	1							3	7	11	17		11				2		2		15	17					10		7	1	3	21
-6	R	15							1		11	12	17		11								11	17		1	3		6		3			13
-8	R	15	1								12	13	17		8	1			1		3		13	17	1		1		1	3	5	3	3	17
-9	R	15							2		8	10	17		14							4	18	17		2	1		15		1		2	21
-10	W	15							4		10	14	17	1	12			1	2				16	17	3	1				5	1	6	1	17
-11	R	15									12	12	17	1	13			2					16	17		5	1		2		2			10
-12	R	16	2							1	9	12	17		11			1			2		15	17			2		11		3		2	18
-13	R	16								2	12	14	17		17								17	17					4		7	1	6	18
-14	R	16	2								10	12	17		14								14	17	1				11					12
-15	R	16	4								6	10	17		15								15	17	1						2		9	12
-17	W	15	2					3		2	2	9	17		11				1				12	17	2				2	3		3	3	13

(continued)

Table IV.-- (Continued, page 3)

Parents, differentials, or F_3 families	Seed color	Results for biologic form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
799-18	W	15									11	11	17	2		1			9				12	17				2	6	4	1			13
-19	R	17	2							4	7	13	17	1	12				1				14	17	1				7		1		3	12
-20	R	17	1				1	4		1	3	10	17		1			10					11	17	1		1		10	5		1		18
-21	R	17	1							1	11	13	17		4			1		1	4	4	14	17	2	1			6		4		7	20
Mindum	W	16	11							2	29	42	17	2	34	4							40	17	4						11		93	108
D5	R	16	3						1	12	10	26	17	3	5			5	4	3	1	1	22	17	5	4	17		85	2	7			120
799-22	R	17	1								13	14	17		16				1				17	17	1				9		5		2	17
-23	R	17	1								9	10	17		15							2	17	17		1			16	3				20
-24	R	17	1					1		2	9	13	17		13				1				14	17					2	4	5	1	4	16
800-1	R	17	1								9	10	17		11				1				12	17	1						3	7	5	16
-6	R	15	2				2				8	12	17		12	1					2		15	17		1			7		8			16
801-5	W	15	1					4	3		4	12	17		6				1	1		10	18	17					2	1	7		5	15
802-1	W	16	2				1	2	1	9		15	16						1		4	4	9											
-2	R	15	3					2			6	11	17		13			1		2			16	17		1			4		7			12
-3	R	17							2	4	7	13	17		9				3				12	17	1					1		11		13
-4	W	15	4							3	4	11	17		10						1		11	17					4		6		7	17
-6	R	17									14	14	17	2	11						1	2	16	17						1	3		14	18
-7	R	15	3								8	11	17		8		1		1			1	11	17					2		2		·9	13
-8	R	15	2								11	13	17		8						1		9	17	1						1	1	8	11
-9	R	15	1					1		5	5	12	17		1						4	4	9	17						1	1		11	13
-10	R	15									12	12	17		14				1				15	17					1		3		6	10
-11	W	17	3					1		3	4	11	17		10			2	3				15	17					5		7			12
803-1	R	15									13	13	17					2	9	2			13	17			2		4	4	4			14
-2	W	15					1	5		5	1	12	17						6		6	9	21	17					1			1	13	15
-4	W	16	1								10	11	16		12			1		1		2	16	17	4	1	1		2		1		2	11
-5	R	17	7							3	2	12	17	2	6				2		1		11	17							2		11	13
-12	R	15	6							1	3	10	17		15								15	17	12								2	14

(continued)

Table IV.-- (Continued, page 4)

Parents, differentials, or F_3 families	Seed color	Results for biologic form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
803-18	W	15	3						2	1	4	10	17		5								5	17									4	4
-19	R	15	1						1	3	9	14	17		13								13	17	2					2	9	1	3	20
-21	R	15	1				4	1			6	12	17		11			1	4		1		17	17	2				6	2	5		1	16
-22	W	15	3							1	5	9	16		9								9											
-25	W	17	1							1	8	10	17		7						1	3	11	17						5	1	2	4	12
-26	R	17									13	13	17		9				1			4	14	17					5	3	3		1	12
-28	R	17	4								8	12	17		11								11	17	1				1		8		3	13
Mindum	W	16					1	1		2	20	24	16	1	69							3*	73											
D5	R	16	6	3			10	2				21	16	5	1	1		6		10	3	6	32											
803-30	W	16	1								10	11	16									8	8											
-33	R	15	7							2	3	12	17	2	1				4		10		17	17	1						3	4	4	12
-34	R	15								2	9	11	17	4	4					2		3	10	17					6				8	14
-36	R	15	1								11	12	17		8				1		1		10	17					7		3	1		11
-37	W	16					3	2	1		5	11	16		11						1	4	16											
-39	R	15									16	16	17		16								16	17							7		7	14
-40	R	17	2						4		5	11	17					3	2		2	7	14	17	9		3	1	6	2				21
-42	W	16	5							4	3	12	16	3	2				1		5	3	14											
-45	W	16						1	1	3	7	12	16		19							1	20											
-46	W	16	7								3	10	16	1	7						1		9	16					4	1	2			7
-48	W	16									13	13	16		10				2				12											
804-7	R	16	2								10	12	16									19	19	16									17	17
-17	R	16	2								11	13	16									18	18	16									17	17
805-1	R	16	2					1		5	5	13	16		13						2	1	16	16		1	4	1	13					19
-4	R	16	1							1	12	14	16		15								15	16					6	2	7			15
-66	R	16	5							1	6	12	16		12			1			4		17	16	2	1			8				2	13
-9	R	16	8								4	12	16	1	14						1		16	16			2	1	10	1	1		2	17
-13	W	16								2	12	14	16	1					3		10	1	15											

* Probably these plants were not pure Mindum owing to mechanical mixture or natural crossing.

(continued)

TableIV.-- (Continued, page 5)

Parents, differentials, or F_3 families	Seed color	Results for biologid form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
805-15	W	16	3		1					4	5	13	16		19								19											
-16	W	16									12	12	16		19								19	16					8					8
-19	R	16	4						1	3	4	12	16		9			1		1	1		12	16	1	2			11	1	3			18
-22	W	16								1	12	13	16		9						2		11											
-25	W	16	3		1			2	1	1	5	13	16	1	21								22											
806-1	W	15	2							11		13	16	1					8		9	2	20	16					4	13				17
-2	W	16						3	1	16	3	13	16		11								11											
Mindum	W	16	8								12	20	16	6	105							1*	112	16	5						6		86	97
D5	R	16	15	2	1		1	1	1	6	2	29	16	13	4	1		1	12	6	18	35	90	16	4	2	20	3	26					55
806-5	R	15	2					1	1	2	6	12	16		1							11	12	16					1	14		1		16
-7	R	16						2	1	7		11	16		10						1	1	12	16						1	4			5
-11	W	16								3	4	7	16		7						1		8	17			2		1					3
-12	W	16	1							2	12	15	16		13				1		1	2	17											
-13	R	15	3							3	7	13	16						9		5		14	16					10		4			14
-14	R	16						1	3	2	6	12	16		5						2		7	16							10		2	12
-16	W	16							5	5	2	12	16	2					5		12		19	16					5	3	8		3	19
-17	W	16									12	12	16		17								17											
-18	R	16	2							2	8	12	16						6		9		15	16					10	2	2			14
-22	R	16	3					3	4		2	12	16		11					2	4	3	20	16	1						3		10	14
-23	R	16	5		1				4			10	16	1	9								10	16			2		6		8	1	1	18
-24	R	16	7								5	12	16		10						2		12	16				1	7					8
-25	R	16	5					2		1	5	13	16	2	10								12	16		1			7	2	1			11
-28	R	16	7								3	10	16	1	15								16	16	1	5			3		2			11
-29	R	16	6	1				1	.1		2	11	16		13					1		2	16	16					4		12		2	18
-30	R	16	1				1	6	1	2	1	12	16		9								9	16					2		3			5

* Probably these plants were not pure Mindum owing to mechanical mixture or natural crossing.

(continued)

Table IV.-- (Continued, page 6)

Parents, differentials, or F_3 families	Seed color	Results for biologic form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
807-1	W	16	5				1				5	11	16		6						9	3	18	16					8		3			11
-7	R	16	1					3	2			6	16	1					3		3	1	8	16					2	2		1		5
-8	R	16	4					6				10	16		2						7	2	11	16				1	2	1	3			7
-10	W	16	6					2		2		10	16		10				2	1	2	2	17	16			2	6						8
-18	R	16	9					2	2	2		15	16		15								15	16		1	4		6			2		13
-19	W	16	2					1		1	9	13	16		8				2		2	1	13											
-21	R	15									13	13	16		14								14	16						10	3			13
-23	R	15	4					3	6		3	16	16		15							5	20	16	1	1			1		14		11	28
808-1	W	16		1			5		4	3		13	16		9						1		10											
-3	R	16	1					1	1	5	2	10	16		13					1	1		15	16	1				1				10	12
Mindum		16								2	14	16	15		30							1*	31											
D5		16		1	1	1	3	4	4	4	3	21	15	2		1		3		8		12	26											
808-10	R	16	1					2	1	5	6	15	16		12						3		15	16			1		3	1	5		1	11
809-4	W	16	4							11	2	17	16		14								14											
-5	R	15									12	12	16		15								15	16	1				12		5		6	24
-6	R	15	4				1		1		6	12	16		17								17	16							7	2	2	11
-8	R	16	6	2	3			1	1			13	16		1				1	9	2	7	20	16	3		5		16		2			26
-10	R	16	7							2	3	12	16		16								16	16					1		8			9
-11	W	16	4						2	4	2	12	16		15								15	16	1			1	2		5			9
-12	W	16	1							1	10	12	16		9								9											
-13	W	16						2	2	5	2	11	16		9						2		11											
-17	W	16									11	11	16	3								3	6											
-18	W	15	4								8	12	16		14								14	16					8	3	3			14
-21	W	16	2								9	11	16	2	10								12	16			2		10					12
-23	W	16									12	12	16	2	11								13											

* Probably these plants were not pure Mindum owing to mechanical mixture or natural crossing.

(continued)

Table IV.-- (Continued, page 7)

Parents, differentials, or F_3 families	Seed color	Results for biologic form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
810-1	R	16	1							7	5	13	16	2	10				1		1	4	18	16			2		8	1	2	3		16
-3	W	16	2							4	9	15	16		7						1	1	9	16					3	4	3		2	12
-7	W	16								1	11	12	16		1	3		1	6		1		12											
-10	W	16	5					5		1	1	12	16		15						3		18	16					4	12	5			21
664-1	W	16							4	3	3	10	15		10				2		1		13											
666-2	W	16						1		2	6	9	15		8							1	9											
-3	W	16						1	4	5	4	14	15		12					1	3		16	17			3		7		5		1	16
-4	W	16								1	6	7	15		9								9											
-6	W	16									8	8	15		6						1	2	9											
-7	W	16					1	2	1	3	2	9	15						4		4		8											
667-4	W	16									6	6	15		16								16											
-5	W	16								2	9	11	15		9								9	17		2			6		1			9
-8	W	16									9	9	15		14								14											
Mindum		16	5					1		9	19	34																						
D5		16	1	1	1		8	1	7			19																						
667-16	W	16									13	13	15		11					1			12											
-17	W	16						3	2	2	4	11	15	1	7				2				10											
-18	W	16					1	1		8		10	15		10			1	1				12											
668-1	W	16	1							2	6	9	15		4	1			1				7											
669-1	W	16								3	7	10	15		14				3		1	1	19											
-6	W	16									12	12	15	1	12								13											
672-1	W	16	3						2	1	7	13	15		9						1	2	12											
-3	W	16								3	11	14	15		14								14											
673-1	W	16								1	13	14	15		13				1		2	1	17	17		2	5		11		2			20
-8	W	16					1		2	2	7	12	15		10	1	1		1		1		14											
675-2	W	16					2	1	3	3		9	15		1	1			5		3	4	15											
-3	W	16						6		6		12	15		1				1		4	4	10											
-11	W	16						3		10		13	15		11				2		2		15											

(continued)

Table IV.-- (Continued, page 8)

Parents differentials, or F_3 families	Seed color	Results for biologic form No. 17											Results for biologic form No. 1											Results for biologic form No. 34										
		Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants	Period of rust development (days)	No apparent infection	Types of infection								Total F_3 plants
				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4				0	1	2	X-	3	X+	4-	4	
676-4	W	16								3	8	11	15		2	1			2	6	4	3	18											
677-8	W	16								6	9	15	15	1	14				1		1	1	18	17	2				2	6	2	5	3	20
-9	W	16		1			1	1	3	4	5	15	15	2	11				1		4		17	17	6	3	1		8	2	1			21
-11	W	16							3	2	7	12	15		14								14											
678-2	W	16						3		6	3	12	15		10	1				1	1	2	15											
-3	W	16						1	4	10		15	15	1	3				4	3	5	2	18	17		8			10					18
-5	W	16						2	3	5	4	14	15		15				1		2		18	17		6	4		12					22
-6	W	16	2								9	11	15						5		4	7	16	17		2	7	1	10		1			21
-7	W	16						9	2	3	1	15	15						2		2	12	16	17					15	3	1			19
-10	W	16							3	5	4	12	15		10				1		1		12											
680-1	W	16	2								4	6	15		10						2		12											
-3	W	16									15	15	15		14								14											
-5	W	16							2	3	10	15	15		11					1	2	6	20	17			1		2	1		3	12	19
-8	W	16					1		4		9	14	15		9	1				3		4	17											
Little Club		16	1								8	9	16									13	13											
Marquis		16								6	4	10	16	2								12	14											
Kanred		16	12	2								14	16	10								1	11											
Kota		16						7		3		10	16								8	7	15											
Arnautka		16								3	11	14	16		9						2	2	13											
Kubanka		16						2		4	7	13	16	2	1							12	15											
Acme		16								5	6	11	16								6	5	11											
Einkorn		16						10				10	16								14		14											
Emmer		16		12								12	16	3	11								14											
Khapli		16	1	3	3							7	16			14							14											

About 50 per cent of the type 4 infections for Form 34 were characterized by well-marked hypersensitiveness surrounding the uredinia. The pustules, however, were large and confluent.