THE RESISTANCE OF TWELVE VARIETIES OF *TRITICUM VULGARE* TO *ERYSIPHE GRAMINIS TRITICI*

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Summary

A genetic study has been made of the resistance of 12 varieties of *Triticum vulgare* Vill. to a South Australian isolate of *Erysiphe graminis tritici*. This collection has been resolved into two pathogenic components which may be differentiated by their reactions on the variety Chul.

The 12 varieties studied fall into three natural groups. Eight varieties of group *A* possess a common gene, Ml_t, which confers resistance to mildew at all stages of growth. Ml_t is completely linked with a gene conferring resistance to race 135AB of *Puccinia triticina* Erikss.

Group *B* is represented by a single variety which derives its mildew resistance from a second gene, Ml_u. This variety is susceptible to *P. triticina* 135AB.

The three varieties of group *C* are resistant to mildew from the three-leaf stage onwards and apparently owe their resistance to a third gene, Ml_s. These varieties are also susceptible to *P. triticina* 135AB.

I. Introduction

During the past quarter of a century, much evidence has been accumulated showing that a high degree of specialization occurs within many obligate pathogens of cereals and other cultivated plants. Only more recently have plant breeders become fully aware of the need for placing the emphasis upon gene-"race" relationships rather than upon large-scale "race"‡ surveys using differential varieties of unknown genetic constitution.

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‡ In plant pathological literature continual reference is made to "physiological races," a name used to designate isolates of pathogenic fungi, each possessing a characteristic range of pathogenicity on a set of so-called differential varieties. Such isolates have originally been made in the field, later to be maintained as clonal lines in a more or less static condition in the laboratory.

On the other hand, the use of the word *race* in genetics has a quite different connotation, being used always for a natural population ("Mendelian population" or "mating group") within which there is a continual exchange of genes during the sexual cycle.

Although physiological race, as a plant pathological term, has the official support of the Sixth International Botanical Congress, 1935, it is now suggested that, taking into consideration the developments in botanical science since that time, the term *race* be retained as a word expressing the genetical concept as outlined above.

If this be agreed upon, then some other term is needed for isolates of pathogenic fungi exhibiting characteristic parasitic qualities. Unfortunately the authors are unable to suggest an appropriate name so that in the present paper such isolates are designated as races.

The studies reported in this paper were undertaken with the object of identifying in 12 varieties of *Triticum vulgare* Vill. the genes for resistance to an isolate of *Erysiphe graminis tritici* occurring at the Waite Agricultural Research Institute, South Australia.

II. Review of Literature

Using Federation as the susceptible parent, Waterhouse (1930) showed that Thew possessed a single dominant gene for resistance to one of two races of *E. graminis tritici* occurring in the glass-house at Sydney University. He noted a linkage between this gene for mildew resistance and one for resistance to "Australian form 1" of *Puccinia triticina* Erikss. Nine other varieties (not specified) were found to possess this combined resistance to the above races of the respective pathogens.

Watson and Baker (1943) subsequently showed that the combined resistance of Thew was also a feature of the variety Kenya 744 and that it was due to a single dominant gene or to two completely linked genes.

Mains (1934) showed that Norka C.I.4377 possessed a single dominant gene for resistance to "U.S.A. form 1" of *E. graminis tritici* which was independent of a dominant gene for resistance to *P. triticina* "form 3." Red Fern was found to have a single dominant gene for resistance to "U.S.A. forms 1 and 2" of mildew, while Hope C.I.8178, which gave variable reactions to "form 1," apparently had a single recessive gene for resistance to this form. Sonora C.I.4293 likewise possessed a single recessive.

Pugsley (unpublished data) revealed the presence of one common gene in the varieties Thew, Kenya C6041 (Kenya 744), and Norka for resistance to the mildew population occurring at the Waite Institute. A second gene was detected in Sonora, and in each of the crosses between Sonora and the abovementioned varieties, dihybrid ratios were secured in F_2 and F_3 populations.

Favret and Vallega (1949) ascribed the resistance of Axminster and Normandie to the Argentine races of *E. graminis tritici* as being due to a simple, almost completely dominant gene segregating independently of a gene governing resistance to *P. triticina* race 5, but linked to that for resistance to *P. triticina* race 20.

Sears (1950), by nullisomic analysis, has located a dominant gene for mildew resistance in Axminster on chromosone XI.

Lowther (personal communications 1951) has used the varieties Axminster C.I.8195, Ulka C.I.11478, Chul C.I.2227, Hope C.I.8178, and Normandie C.I.12747 as differentials to distinguish 10 physiologic races in U.S.A. From his data, it is evident that Axminster and Normandie differ in genetic constitution since the latter is resistant to a number of races to which the former is susceptible. Lowther reports Huron C.I.3315, Norka C.I.4377, and Converse C.I.4141 as reacting similarly to each of these 10 races; however, the latter finding is in disagreement with that of Taylor, Rodenhiser, and Bayles (1949) who reported that Converse was resistant to a mildew "collection" to which both Axminster and Norka were susceptible.

III. Materials and Methods

The following mildew-resistant varieties were used as parents in a series of crosses made during 1950 and 1951:

Thew	An Australian variety from ((Sinew × Improved Fife) × (Improved Fife × Hussar)) × Blount's Lambrigg selection.
Kenya C.6041 (N.S.W. Department of Agriculture)	Introduced from Kenya as B.F.4.2D.30.B.2 (L). Identical with Kenya 744 (Sydney University), and P.I.124737 (United States Department of Agriculture).
Axminster C.I.8195	Developed by Samuel Larcombe of Birtle, Manitoba, Canada, and believed to be a natural cross between Marquis and an unknown variety.
Converse C.I.4141	Origin not known.
Birdproof	Introduced by the N.S.W. Department of Agriculture from Basutoland, South Africa.
Huron C.I.3315	Derived from a cross made in 1888 between White Fife and Ladoga at the Central Experimental Farm, Ottawa, Canada.
Norka C.I.4377	Originated from a pure-line selection of common wheat separated from a plot of Kubanka durum wheat in 1908 at Akron, Canada.
Normandie	Derived from a cross Vilmorin 27 × Hybride 40 made in 1935. Leblond Villegats (Euré.) in France.
Ulka C.I.11478	Obtained by the Dickinson, North Dakota, U.S.A., Station, from a farmer who introduced it from Russia.
Sonora C.I.3036	Brought to the United States from Magdalena Mission, Northern Sonora, Mexico.
Indian C.I.4489	Origin not definitely known. Probably the result of a natural hybrid between Sonora and some other variety. Mildew-resistant selection made at the Waite Institute.
Sturgeon C.I.11703	Produced by the Wisconsin Agricultural Experimental Station, U.S.A., from a cross between Progress and Marquis.

The Australian variety Federation was used as the only susceptible parent.

The original isolation of *E. graminis tritici* was made from the variety Federation at the Waite Institute in 1940, and since then it has been maintained on that variety. Over the years 1940-51, this isolate gave consistent reactions on Thew, Kenya C.6041, Norka, Sonora, and Federation, and there was no evidence to indicate that it was other than a single physiologic race. During the winter months of 1951, Chul C.I.2227 was tested on several occasions, and gave a susceptible reaction. In April 1952, however, the anomalous behaviour of Chul during routine tests at the Waite Institute led to the separation of two races from the mildew population. At that time Chul gave a resistant reaction after the normal incubation period of 8-10 days; but pustules of mildew began to appear after 3 wk of exposure to infection from Federation plants growing alongside. Apparently the mildew on Federation at that time was composed of two races—one capable of attacking Chul and the second incapable of attacking that variety. These races have been designated *P* and *P*-1 respectively. The latter was freed from the original race *P* by three successive rapid transfers on Federation.

A culture of *P*-1 was taken to Canberra in May 1952, and tests in the glass-house during the winter of that year indicated that it remained free from race *P*. Reactions of the 12 resistant parental varieties to *P*-1 at Canberra were consistent with those obtained previously with both *P* and *P*-1 at the Waite Institute.

The susceptibility tests were carried out with seedling plants grown in the glass-houses of the Waite Institute, Adelaide, and the Division of Plant Industry, C.S.I.R.O., Canberra. Seedlings were grown in seed boxes and inoculated at the one- to two-leaf stage by dusting with spores from heavily infected plants of Federation. Several seedlings of the parental varieties and of Federation were included in each test. By this method 100 per cent. infection of susceptible seedlings was readily obtained. All 1951 tests were conducted at Adelaide using race *P* (with possibly small amounts of *P*-1 present). In 1952, some tests were conducted at Adelaide in the presence of both races, and the tests at Canberra were carried out with *P*-1 alone. There was no evidence to indicate that any of the varieties used, or their hybrid progenies, reacted differentially towards the two races.

In order to determine which varieties possessed the combined resistance of Thew to leaf rust and mildew, the parental varieties were tested against *P. triticina* race 135AB (Waterhouse 1952). Inoculum for the Adelaide tests was isolated from the field at the Waite Institute in November 1950, while that for the Canberra tests originated from a culture supplied by Dr. I. A. Watson of the Sydney University. A race of leaf rust capable of attacking Thew (race 138BB, Waterhouse 1952) isolated from the field at the Waite Institute in 1951 was also studied. The two races of *P. triticina* were used in examining linkage relationships between mildew and leaf rust resistance in certain crosses as outlined in Sections IV (*b*) and (*c*).

Seedlings for rust and mildew susceptibility tests were grown in 6-in. pots. The rust inoculum was applied to the first leaf and the seedlings then held for 24 hr in a humid chamber. The mildew inoculum was applied 2 days later. There was no visible evidence of an interaction in the symptom expression of the two diseases.

IV. Experimental Results

Varietal reactions to the two races of *E. graminis tritici* and to the two races of *P. triticina* are given in Table 1.

TABLE 1

REACTION OF WHEAT VARIETIES TO RACES *P* AND *P*-1 of *E. GRAMINIS TRITICI* AND TO RACES 135AB AND 138BB OF *P. TRITICINA*

R=resistant; S=susceptible

Variety	Reaction to *E. graminis tritici*		Reaction to *P. triticina*	
	Race *P*	Race *P*-1	Race 135AB	Race 138BB
Group A				
Axminster	R	R	R	S
Birdproof	R	R	R	S
Converse	R	R	R	S
Huron	R	R	R	S
Kenya C6041	R	R	R	S
Norka	R	R	R	R
Normandie	R	R	R	S
Thew	R	R	R	S
Group *B*				
Ulka	R	R	S	S
Group *C*				
Indian	R*	R*	S	S
Sonora	R*	R*	S	S
Sturgeon	R*	R*	S	S
Federation	S	S	S	S
Chul	S	R	—	—

* These varieties characteristically developed some mildew if exposed to infection at the single-leaf stage, but were more resistant if grown to the three-leaf stage before inoculation. Sturgeon usually developed small lesions on the leaf sheath.

(*a*) *Inheritance of Mildew Resistance*

The resistant varieties have been classified into three groups (Table 1) of which group *A* comprises varieties resistant to mildew at all stages of growth and to *P. triticina* 135AB, group *B* (one variety) is resistant to mildew at all stages of growth but susceptible to *P. triticina* 135AB, and group *C* is resistant to mildew from the three-leaf stage and susceptible to *P. triticina* 135AB. The inheritance studies are discussed for each group in turn and for intra- and intergroup crosses. Results are summarized in Table 2.

(i) *Group* A *Crosses with Federation and Intragroup Crosses*.—This group comprises Axminster, Birdproof, Converse, Huron, Kenya, Norka, Normandie, and Thew.

The F_1 plants from crosses between these varieties and Federation were mostly grown in the field at the Waite Institute, a few being grown in the glasshouse during the winter. The absence of mildew infection in all cases indicated the complete dominance of resistance.

TABLE 2

CLASSIFICATION OF F_2 SEGREGATES FOR THE CROSSES INDICATED WITH RESPECT TO MILDEW REACTIONS

For parental reactions, see Table 1. For each cross: 1st line, 1951 Adelaide; 2nd line, 1952 Adelaide; 3rd line, 1952 Canberra. R = resistant; S = susceptible.

P value for all ratios exceeds 0.05

		Group *A*								Group *B*	Group *C*		
	Parent	Axminster	Birdproof	Converse	Huron	Kenya	Norka	Thew	Normandie	Ulka	Sonora	Sturgeon	Indian
	Federation	71R:23S 87R:23S 77R:34S	— 106R:32S —	530R:172S — —	71R:22S — 81R:29S	555R:183S 109R:38S —	520R:185S 135R:40S 286R:103S	200R:79S — —	— 333R:26S* 436R:26S	— 155R:54S* 186R:52S	— — 79R:34S	— — 86R:30S	308R:108S 59R:30S 89R:33S
Group *A*	Axminster		— — —	— — —	— — —	— — —	— — —	— 135R:0S 117R:0S	— — —	— — —	— — 109R:5S	— — —	— — —
Group *A*	Birdproof			— — 114R:0S	— 128R:0S 229R:0S	— 121R:0S 119R:0S	— 109R:0S 120R:0S	— 109R:0S 231R:0S	— 106R:0S 241R:0S	— — —	— — —	— — —	— — —
Group *A*	Converse				235R:0S — —	240R:0S — —	— 177R:0S 235R:0S	225R:0S — —	— 107R:0S 239R:0S	— — —	325R:81S† — —	88R:7S — —	354R:25S — —
Group *A*	Huron					235R:0S — —	— 154R:0S 111R:0S	240R:0S — 109R:0S	— 118R:0S 237R:0S	— 253R:16S* 96R:3S	— 111R:8S* 222R:16S	303R:26S — —	227R:10S — —
Group *A*	Kenya						— 82R:0S 115R:0S	203R:0S — —	— 212R:0S 481R:0S	— 371R:16S* 333R:22S*	— 100R:6S* 228R:12S	— — —	— — —
Group *A*	Norka							73R:0S — —	— 111R:0S 333R:0S	— — —	— — —	275R:53S† 82R:17S† —	216R:11S — —
Group *A*	Thew								— — —	— 71R:3S* 90R:6S	150R:9S — —	— — —	467R:27S — —
Group *A*	Normandie									— — 208R:0S	— — 185R:4S	— — 188R:4S	— 300R:8S* 234R:4S
Group *B*	Ulka										— 218R:19S 227R:12S	— — —	— — —
Group *C*	Sonora											— — 237R:0S	240R:0S — —
Group *C*	Sturgeon												231R:0S — 233R:0S
Group *C*	Indian												

For each cross:
first line = 1951 Adelaide
second line = 1952 Adelaide
third line = 1952 Canberra
R = resistant
S = susceptible

Expected Ratios

Group *A* (Normandie excepted)	×	Federation	3:1
Normandie	×	Federation	15:1
Group *B*	×	Federation	3:1
Group *C*	×	Federation	3:1
Group *A* (Normandie excepted)	×	Group *B*	15:1
Group *A* (Normandie excepted)	×	Group *C*	15:1
Normandie	×	Group *B*	63:1
Normandie	×	Group *C*	63:1
Group *B*	×	Group *C*	15:1

P value for all ratios exceeds 0.05

* Resistant class includes some plants with slight infection of mildew.

† Expected ratios 13:3 rather than 15:1.

F_2 progenies were readily classified into resistant and susceptible classes which reacted like the respective parents in each case and, with the exception of Normandie, monohybrid ratios were obtained. There was no evidence of inconsistencies between tests using race *P* and race *P*-1.

In the cross Normandie × Federation, susceptible segregates constituted about 1/16 of the F_2 population, indicating the presence of two pairs of independently segregating genes. On one occasion an intermediate class was present (93 resistant, 14 intermediates, 7 susceptible), suggesting a 13:2:1 ratio rather than a 15:1, in which case it would appear that one of the two genes in Normandie is incompletely dominant for resistance.

Although undoubtedly Birdproof possesses the Thew gene, some evidence has been obtained suggesting the presence of additional genes in this variety. A further examination of Birdproof crosses is being made with a view to securing confirmatory evidence on this aspect.

With regard to intragroup crosses, in no case did susceptible segregates appear in the F_2, indicating that the eight varieties share a common gene. The reactions of these varieties to leaf rust support the view that this gene is identical with that originally studied in Thew by Waterhouse (1930).

(ii) *Group* B: *Ulka.*—F_1 plants of Ulka × Federation developed a trace of mildew infection at the Waite Institute when tested with race *P* although such heterozygotes were not always separable from the homozygous resistant class in F_2 progenies. At Canberra, F_1 plants were as resistant as the Ulka parent when tested with race *P*-1. The F_2 segregation in all cases was indicative of a monogenic difference.

(iii) *Group C Crosses with Federation and Intragroup Crosses.*—This group includes Indian, Sonora, and Sturgeon, the analysis of which proved more difficult. Because the parents exhibited a partial susceptibility when inoculated prior to the three-leaf stage, the seedlings were usually raised in a separate glass-house and inoculated at a later stage of development than was the case with crosses involving groups *A* and *B*. The F_1 hybrids between these varieties and Federation were intermediate in resistance between the respective parents, and classification of F_2 progenies was often difficult, due apparently to differences in expressivity of the heterozygote class. Intragroup crosses indicated the presence of a common gene in the three varieties, since no fully susceptible segregates were obtained. The F_3 data for Federation × Indian indicated a monogenic difference, and the hypothesis of a common major gene, incompletely dominant, is advanced for these three varieties.

(iv) *Intergroup Crosses.—Groups* A *and* B. Except for the special case Normandie, susceptible segregates appeared in F_2 progenies of these crosses, indicating the non-allelic nature of the Ulka gene with that of the Thew gene in the group *A* varieties. The data were in agreement with a 15:1 ratio.

No susceptible segregates appeared in a Normandie × Ulka F_2 population of 208 plants; however, a larger population would be necessary to differentiate between a 63:1 and a non-segregating population. At present, then, it is not possible to say whether the second gene of Normandie is identical with the Ulka gene.

Groups A *and* C. Again, susceptible segregates appeared consistently in F_2 progenies of all the crosses examined. On several occasions segregates with slight mildew development were detected and although these were usually classified with the resistant segregates, in some cases they were more readily included with the susceptible segregates, giving ratios approximating 13:3 rather than 15:1.

In each of the three crosses involving Normandie, the data were in agreement with a 63:1 ratio, indicating that each of the two genes in Normandie was different from the group *C* gene.

Groups B *and* C. Segregation of susceptible plants occurred in the only cross examined, namely, Ulka × Sonora, indicating the non-allelic nature of the Ulka gene with that of the Sonora gene.

TABLE 3

CLASSIFICATION OF F_2 SEGREGATES OF THE CROSSES NAMED WITH RESPECT TO MILDEW AND LEAF RUST 135AB REACTIONS

For parental reactions, see Table 1

Cross	Mildew Resistant		Mildew Susceptible		Ratio	Value of *P* for Ratio Indicated
	Leaf Rust Resistant	Leaf Rust Susceptible	Leaf Rust Resistant	Leaf Rust Susceptible		
Federation × Axminster	148	0	0	57	3:1	>0·3
Federation × Converse	130	0	0	43	3:1	>0·99
Thew × Federation	112	0	0	47	3:1	>0·3
Federation × Huron	80	0	0	30	3:1	>0·5
Normandie × Federation	80	23	0	6	12:3:0:1	>0·8
Norka × Federation	85	0	15	9	12:0:3:1	>0·3
Indian × Converse	131	31	0	12	12:3:0:1	>0·9
Thew × Indian	123	36	0	12	12:3:0:1	>0·5
Sonora × Thew	126	24	0	9	12:3:0:1	>0·3
Thew × Huron	109	0	0	0		
Thew × Birdproof	111	0	0	0		
Huron × Birdproof	112	0	0	0		
Normandie × Norka	103	0	0	0		

(*b*) *Association of Mildew Resistance and Resistance to* P. triticina *Race 135AB*

Earlier reference has been made to the fact that all the mildew-resistant varieties of group *A* were resistant to *P. triticina* race 135AB. In view of the reported linkage between resistance to these pathogens in Thew and Kenya, one would expect a similar relationship to hold for the other varieties of this group. Evidence for such complete linkage with respect to the varieties Thew, Axminster, Converse, and Huron when crossed with Federation is presented in Table 3. In each instance, mildew-resistant segregates were resistant to leaf rust and mildew-susceptible segregates were susceptible to leaf rust, there being no recombination classes.

The results from other crosses also listed in Table 3 (Indian × Converse, Thew × Indian, and Sonora × Thew) clearly indicate the segregation of two genes for mildew resistance, one of which is linked to that conferring resistance to race 135AB of leaf rust.

Evidence of linkage in the varieties Norka and Normandie is also indicated but obscured by the segregation of additional genes. In the cross Norka × Federation, all mildew-resistant segregates were also resistant to leaf rust, but the data indicate that Norka possesses a second gene for leaf-rust resistance which is not associated with mildew resistance. With regard to Normandie, earlier results have indicated a segregation of additional genes for mildew resistance when this variety is crossed with Federation. That one of these genes is associated with leaf-rust resistance while the other is not, is clear from the data presented in Table 3.

TABLE 4

CLASSIFICATION OF F_2 SEGREGATES OF THE CROSS NORKA × FEDERATION WITH RESPECT TO MILDEW AND LEAF RUST 138BB REACTIONS

For parental reactions, see Table 1

Cross	Mildew Resistant		Mildew Susceptible		Ratio	Value of *P* for Ratio Indicated
	Leaf Rust Resistant	Leaf Rust Susceptible	Leaf Rust Resistant	Leaf Rust Susceptible		
Norka × Federation (Adelaide)	34	19	13	6	9:3:3:1	>0·2
Norka × Federation (Canberra)	75	40	36	11	9:3:3:1	>0·05

(*c*) *Independent Inheritance of Mildew Resistance and Resistance to* P. triticina *Race* 138*BB*

From the data presented in Tables 1 and 3 it is evident that Norka possesses leaf rust resistance additional to that found in the other varieties of Group *A*; this would also be concluded from the data of Mains (1934) who found independent inheritance of mildew resistance and leaf rust resistance in crosses between Norka and susceptible varieties. The data of Table 4, where race 138BB was used in the place of race 135AB of leaf rust, lend evidence in support of Mains's work and show that Norka carries a second gene for leaf rust resistance which is inherited independently of the Thew gene. This second gene gives resistance to both races 135AB and 138BB of leaf rust.

V. DISCUSSION AND CONCLUSIONS

As a result of the studies here reported, two physiological races have been isolated from the population of *E. graminis tritici* at the Waite Institute, South Australia. These races may be distinguished by their reactions on the variety

Chul C.I.2227, which is susceptible to the isolate designated race *P* and resistant to that designated race *P*-1. Since race *P*-1 has been studied at Canberra in the absence of race *P* and no results obtained which conflicted with the Adelaide results, it may be stated that the inheritance of resistance in the varieties studied follows a similar pattern with respect to both races.

Reviewing the results of the genetic analysis, it is concluded that 11 of the varieties differ from the susceptible Federation by one gene, while the 12th variety, Normandie, differs by two genes. The possibility that Birdproof possesses additional resistance has been recognized, but final conclusions with respect to this variety must await confirmatory evidence. Furthermore, a number of the varieties have been shown to contain a common gene for resistance.

Three distinct genes for mildew resistance have been identified, with a possible fourth gene occurring in Normandie. In assigning symbols to these genes, the system of nomenclature suggested by Briggs and Stanford (1938) in work on mildew resistance in barley has been adopted. The need for a standard system of genetic nomenclature and symbols for the wheat plant has long been recognized although as yet no general agreement has been reached. The present designations should, therefore, be regarded as tentative only.

Ml_t, Ml_u, and Ml_s are suggested as designators of the genes for resistance common to varieties of groups *A*, *B*, and *C* respectively, and are so named because they were first detected in the varieties Thew, Ulka, and Sonora, respectively. Until its identity can be established positively, the additional resistance of Normandie is symbolized by Ml_u.

The genetic constitution of the 12 resistant varieties and Federation may be written:

Group *A*				Group *B*			
Axminster	Ml_t	ml_u	ml_s	Ulka	ml_t	Ml_u	ml_s
Birdproof	Ml_t	ml_u	ml_s				
Converse	Ml_t	ml_u	ml_s	Group *C*			
Huron	Ml_t	ml_u	ml_s				
Kenya C. 6041	Ml_t	ml_u	ml_s				
Thew	Ml_t	ml_u	ml_s	Indian	ml_t	ml_u	Ml_s
Norka	Ml_t	ml_u	ml_s	Sonora	ml_t	ml_u	Ml_s
Normandie	Ml_t	Ml_u?	ml_s	Sturgeon	ml_t	ml_u	Ml_s
				Federation	ml_t	ml_u	ml_s

Since the 12 mildew-resistant varieties fall into three groups with respect to the races studied, one would expect some degree of correlation in the behaviour of the varieties of each group towards other races of mildew. Evidence of such a correlation has been given by Lowther (personal communication, 1951) who reports that Norka, Converse, and Huron reacted to 10 physiologic races in a manner quite similar to Axminster. Normandie was resistant to all races to which the latter group were resistant, but it was also resistant to additional races, no doubt because of the presence of its second gene for resistance. In no case has Normandie been susceptible to races incapable of attacking Axminster.

Taylor, Rodenhiser, and Bayles (1949) found Indian and Sturgeon to react alike to three physiologic races, but with respect to group *A* varieties, their results are at variance with expectation, since Converse was resistant and Axminster and Norka susceptible to one of their three races.

Newton and Cherewick (1947) reported parallel reactions of Norka and Axminster to three Canadian races and, to the extent to which it was tested, Thew reacted similarly.

Certain anomalous results have been reported for Huron by Mains (1933), Vallega and Cenoz (1941), Newton and Cherewick (1947), and Taylor, Rodenhiser, and Bayles (1949), but these discrepancies are almost certainly caused by genetic differences between the strains of Huron used. Local experience confirms the work of Taylor, Rodenhiser, and Bayles (1949) in demonstrating clear differences in mildew reaction between Huron R.L. 20 (C.I. 12663) and Huron C.I.3315.

The results of inheritance studies are in close agreement with those reported by Waterhouse (1930), Mains (1934), Watson (1943), and Vallega and Favret (1950), so that it is now well established that the Thew gene for mildew resistance, as it exists in several varieties, is very closely, if not completely linked with a gene for resistance to certain races of *P. triticina*, and at the same time inherited independently of genes conferring resistance to other leaf rust races.

As with mildew, a similar correlation of behaviour towards other leaf rust races might also be expected with the varieties of group *A*. This expectation was realized in the present study with respect to races 135AB and 138BB, and is additionally supported by the results of Vallega (1944) who found Axminster, Normandie, and Thew to react in essentially the same way to six Argentine leaf rust races. However, Waterhouse (1952) describes Norka as susceptible and Thew as resistant to race 10A of *P. triticina*.

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