RESISTANCE IN RYE TO LEAF RUST, PUCCINIA DISPERSA ERIKSS.[1]

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INTRODUCTION

The leaf rust of rye, *Puccinia dispersa* Erikss., and its host are coextensive, for this disease has been found practically in all parts of the world where rye is grown. The literature on this rust refers to it under several different names. It belongs to that group of leaf rusts of cereals and wild grasses to which the name *P. rubigo-vera* (D C.) Wint. was for a long time applied. Eriksson and Henning (*9*)[3] separated this species into two, *P. glumarum* (Schm.) Erikss. & Henn., the stripe rust, and *P. dispersa* Erikss., the brown rust of cereals and wild grasses. On account of differences in hosts, a number of races were recognized within the brown rust by Eriksson (*6*), that on rye being designated as *P. dispersa* f. sp. *secalis*. Later the races on the other cereals and the wild grasses were raised to specific rank by Eriksson (*7*) and given binomial names, leaving the name *P. dispersa* for the rust found on rye. As such it has been most widely known in the literature which deals with this fungus as the cause of a disease of rye. Still other names, however, have been applied to it in mycological literature, such as *P. secalina* Grove, *P. asperifolii* (Pers.) Wettst., and *Dicaeoma asperifolii* (Pers.) Kuntze. A full list of such names is given by Arthur and Fromme (*1*) in the North American Flora.

The biology of this rust has been more or less completely worked out. *Puccinia dispersa* was shown by DeBary (*2*) to produce its aecia on *Anchusa officinalis* and *A. arvensis*, results which were duplicated by a number of others both in Europe and in this country. Apparently, however, this aecial stage usually is not necessary for the survival of the rust from year to year, since it has been observed to live over winter in the rye plant itself by Baudyš (*3*), Treboux (*13*), and others in Europe and by Carleton (*4*), Christman (*5*), and others in this country. That the other cereals and the wild grasses play no part in the overwintering and spread of this disease of rye is evident from the work of Eriksson (*6*, *7*) and others, who have found that this rust is closely restricted to rye.

The severity of the disease varies in different regions, according to climatic conditions. Its severity also varies from year to year in any one locality as weather conditions vary, but it is always present to some extent. Under favorable conditions, such as years with mild winters and

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[2] The writers wish to acknowledge the efficient assistance of Mr. Leroy E. Compton, Junior Pathologist, Office of Cereal Investigations, in the laborious task of inoculating seedlings.

[3] Reference is made by number (italic) to "Literature cited," p. 251–252.

early springs with cool nights and heavy dews, the rust develops to a conspicuous extent in the principal rye-growing districts, so that by heading time the plants have a reddish appearance from the development of the uredinia of the rust. The rye plant, however, is not killed by the disease, and shriveling of the kernels by this rust has never been noted. Loss in yield is difficult to estimate, since the general prevalence of the rust does not permit any basis for comparison. On the other hand, it is hardly probable that heavy infections do not cause loss, for such infections destroy much photosynthetic tissue, draw heavily on the plant's supply of food material in the development of the rust and especially in its large spore production, and increase evaporation through the rupturing of the epidermis of the rye leaves. All these are factors which vary with the amount of infection, the vigor of the host plant, the condition of the soil, and the temperature and humidity of the atmosphere. As a result, opinions vary as to the amount of damage which may be produced. That the aggregate loss, however, may be considerable, is shown by the estimate made by the Plant Disease Survey of the United States Department of Agriculture [4] for the year 1919. This is based upon reports from the various pathologists throughout the United States, and, therefore, should be a fairly accurate average. According to this estimate, the loss due to the leaf rust of rye in the United States for 1919 was placed at 538,000 bushels, a third of the estimated reduction of yield of rye from all diseases in that year.

As with other rusts of the small grains, there is no feasible method of controlling leaf rust of rye by fungicides. Because of rather general winter survival of the rust in this country, elimination of the alternate host would be of little benefit, even if the latter occurred to any extent. Consequently, the discovery or development of a resistant strain of rye apparently offers the only promise of control of this disease. While the investigations of a number of workers have determined the susceptibility of rye as a species to specialized races of *Puccinia graminis* Pers. and *Erysiphe graminis* D C., as found on the other cereals and grasses, apparently no study has been made to determine whether varietal or individual differences exist in rye as to suceptibility to diseases which are specific to it. A few general field observations have been recorded. Sorauer (*11*) lists eight rye varieties as susceptible to "rust" in Germany and nine varieties as resistant. Vavilov (*15*) states that opinions vary as to the resistance of rye to *P. dispersa*, but that Jaczewski holds Champagne and the ordinary "bushy" variety to be resistant and Noviko notes resistance to leaf rust in Zealand, Danish Kampin, Probst, and Petkus rye.[5] Eriksson (*8*), in the case of the snow-mold disease, states that Petkus rye is resistant, while Zealand is susceptible.

As Vavilov (*15*) and others have pointed out, rye is a cross-pollinated plant with no sharply defined botanical varieties, the commercial varieties differing in being constituted of somewhat different complexes. Under such conditions, sharp varietal differences as to rust resistance are hardly to be expected, and the detection of resistant strains in such complexes is difficult, especially under field conditions, where the plants are intermingled so that individuals are not easily distinguished. The

[4] U. S. DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. PLANT DISEASE SURVEY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1919. In U. S. Dept. Agr., Bur. Plant Indus., Plant Disease Bul. Sup. 12, p. 307-332. 1920.

[5] The writers wish to acknowledge the kindness of Mr. M. N. Levine, Assistant Pathologist, Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture, in translating from the Russian Vavilov's statements concerning rust resistance in rye.

results reported in this paper were obtained through a study of rye seedlings in pot culture in the greenhouse, where individual differences are more easily distinguishable. The employment of this method has resulted in bringing out differences in resistance and gives promise of being of considerable importance in the improvement of rye through the development of disease-resistant strains.

DISCOVERY OF RYE RESISTANT TO LEAF RUST

In the fall of 1920, three kernels from a rye head, supposedly fertilized by wheat pollen in the experimental nurseries at Washington, D. C., were sown in the greenhouse of the Department of Botany, Purdue University Agricultural Experiment Station, at La Fayette, Ind. The resulting plants were there inoculated with the leaf rust of wheat, *Puccinia triticina* Erikss., and the leaf rust of rye, *P. dispersa*. Plants grown from seed from an open-fertilized head of the parent rye plant and from the variety of wheat from which pollen had been used in pollinating the rye head were used as controls. The inoculation with the leaf rust of wheat produced heavy infection on the wheat control but only slight infection on the three supposed hybrids and on the rye control. Inoculation with *P. dispersa*, on the other hand, produced no infection on the wheat control, while on the rye control, one plant, No. 10, was highly susceptible (Pl. 1, D) and another, No. 11, showed some resistance (Pl. 1, E), as indicated by the hypersensitive areas surrounding the uredinia. The three supposed hybrids showed an even greater variation, one plant, No. 7, being as susceptible (Pl. 1, C) as the susceptible control; the second, No. 9, being highly resistant (Pl. 1, A), as shown by the definite hypersensitive areas accompanying the uredinia; while the third, No. 8, was practically immune (Pl. 1, B) showing only a few small hypersensitive areas. Thirty-three other plants from open-fertilized seed of the parent rye plant were then inoculated with the leaf rust of rye, 19 showing a high susceptibility similar to that of plants Nos. 7 and 10, 5 showing some slight signs of resistance, 5 showing a resistance similar to Nos. 9 and 11, and 4 a high resistance similar to No. 8. The similarity in action of the supposed hybrids and the plants grown from open-fertilized rye, at once threw doubt upon their hybrid nature. When grown to maturity all proved to be pure rye, as was indicated by their reaction to the rust.

SECOND GENERATION RESULTS FROM RESISTANT PLANTS

The first generation of the progeny from plants 7, 8, 9, and 10 has been studied as to susceptibility to leaf rust, in an attempt to throw some light on the nature and inheritance of resistance, with the ultimate object of obtaining pure rust-resistant strains of rye. In the spring of 1921, plants 7, 8, 9, and 10 were selfed by bagging the heads of each plant separately, and were crossed in various combinations by bagging the heads of two plants together in combinations as shown in Table I. From the seed obtained from these plants, selfed, crossed, and open-fertilized, 596 plants were raised in the greenhouse at La Fayette, Ind., in the fall of 1921. Each was grown in a 3-inch pot, and when in about the third or fourth leaf, was tested as to its susceptibility to leaf rust. After being studied as to their susceptibility, a select few of each of the principal types were transplanted to 10-inch pots and were selfed and crossed in various combinations again in the spring of 1922. The re-

maining plants were all transplanted to the field, where they also were selfed and crossed in the spring of 1922, thereby furnishing considerable material for further study.

TABLE I.—*Number of seeds of rye obtained by selfing and by crossing plants 7, 8, 9, and 10 in various combinations*

Plant No.	Treatment.	Number of heads.[a]	Number of kernels produced.
7	Selfed	2	8
8	.....do	2	0
9	.....do	2	0
10	.....do	5	3
7	Crossed by 8	1	9
7	Crossed by 9	2	6
7	Crossed by 10	1	17
8	Crossed by 7	1	15
8	Crossed by 9	5	105
9	Crossed by 7	2	16
9	Crossed by 8	5	46
10	Crossed by 7	1	4
	Total	.....	229

[a] The remaining heads in all cases were open-fertilized and produced a total of 367 seeds.

Material differences were found in types of susceptibility in the specimens studied. Nearly all kinds of intergradation between extreme susceptibility and practically complete immunity were noted. These, however, may be divided into about nine main types as shown in Plate 2, A–I.[6] Thus one group showed a high susceptibility (Pl. 2, A) as indicated by the very large size and dark color of the uredinia, approaching in appearance those of *Puccinia graminis*. Under greenhouse conditions this type usually produced from the outer portion of the mycelium a more or less perfect ring of uredinia encircling the one or two first formed. Another group (Pl. 2, B) showed a somewhat less vigorous development, the uredinia being smaller, somewhat lighter in color, and the encircling uredinia being produced less frequently. A few individuals, having a type of susceptibility very similar to the last, showed also a few small uredinia in hypersensitive areas (Pl. 2, D). This condition may possibly indicate the presence of more than one strain of the rust in the culture used or may represent a distinct type. Another group (Pl. 2, E) had uredinia of fair size similar to the preceding, differing in that, while the host tissue in the infected areas did not show any especially deleterious effect, the tissue immediately surrounding these areas became chlorotic and in some cases brown, resulting in the infected areas appearing as green islands. Another group (Pl. 2, C), although having fairly large uredinia, showed a lack of normal adjustment between host and rust in the more or less mottled or chlorotic condition of the host in the infected areas. All of the remainder showed pronounced resistance as indicated by hypersensitive areas which developed in the infected spots. There

[6] Plant 8 (Pl. 1, B) is of the same type of susceptibility as that shown in Plate 2, I; plant 9 (Pl. 1, A) as that in Plate 2, H; plant 11 (Pl. 1, E) as that in Plate 2, F; plants 7 and 10 (Pl. 1, C, D,) as those in Plate 2, A or B. Leaves of the parent plants 7, 8, 9, and 10 were photographed natural size, shortly after infection had appeared, while the types given in Plate 2 were photographed, enlarged two diameters, after the rust had reached its fullest development. This accounts for the single scattered uredinia shown on the susceptible parents and the encircling uredinia in type A, Plate 2.

were various degrees of resistance among these, some having uredinia of normal size each surrounded by a large, sharply defined killed area (Pl. 2, F); others having uredinia much reduced in size but usually accompanying each hypersensitive area (Pl. 2, G); still others in which the hypersensitive areas were numerous and definite but only occasionally containing a small uredinium (Pl. 2, H); and finally those where the only sign of infection was a few more or less indefinite hypersensitive areas, no uredinia being produced (Pl. 2, I). In all cases where hypersensitive areas were present, they were of fairly good size, nothing which might be called flecking apparently being produced.

Vavilov (*14*) gives a system of classification for the types of susceptibility shown by wheat varieties to the leaf rust of wheat, *Puccinia triticina*, a rust very similar in many ways to the leaf rust of rye. He states that this system is a modification of that used by Eriksson, in which five degrees are recognized and are designated by numerals, from 0 (no pustules) to 4 (very pronounced susceptibility). Vavilov, besides using the number of pustules produced, considers the character of development of the fungus of importance, such as the presence of killed areas with or without uredinia. A somewhat similar system of classification has been used by Stakman and Levine (*12*) for the susceptibility of wheat varieties to stem rust, *P. graminis*. In a similar system of classification, the types of leaf rust infection of rye should be arranged as follows:

0. No uredinia formed; hypersensitive areas sometimes present and definite, sometimes faint or absent. Plate 2, I.

1. Uredinia few, minute, in the center of definite hypersensitive areas; few to many hypersensitive areas without uredinia. Plate 2, H, G.

2. Uredinia fairly abundant, moderate in size but always surrounded by hypersensitive areas; hypersensitive areas seldom without uredinia. Plate 2, F.

3. Uredinia abundant, moderate in size, without hypersensitive areas but in some cases surrounded by slightly chlorotic tissue. Plate 2, C, B.

4. Uredinia abundant, very large, hypersensitiveness absent but uredinia occasionally in green islands. Plate 2, A, E.

X. A combination of several of the above types appearing on the same leaf, some uredinia large and without hypersensitiveness, others small and accompanied by hypersensitive areas.[7] Plate 2, D.

The manner of inheritance of rust resistance can not be determined from the results thus far secured. The results obtained from the crosses between the two resistant plants 8 and 9, however, are of interest at this time. From the seed obtained as the result of these crosses, 111 plants were grown. Of these, 2 showed a high susceptibility like A, Plate II; 7 were like B; 9 like C; 11 like D; 19 like F; 38 like G; 17 like H; and 8 like I. In other words, two rye plants showing high resistance, when crossed may produce in their offspring almost all degrees of susceptibility. As shown in Table I, the other crosses and the selfs furnished only 78 kernels altogether. The plants grown therefrom did not furnish additional evidence from which definite conclusions could be drawn. Studies of the inheritance of susceptibility and resistance are being continued with this material.

[7] In some cases this mixture of types of infection may indicate a mixture of strains of the rust; but reinoculations in a few cases with the large uredinia from such mixed types have continued to give the mixed type. These cases, in consequence, would fall into the heterogeneous class X established by Stakman and Levine (*12*).

RESISTANCE OF RYE VARIETIES TO LEAF RUST

Further investigations concerning the susceptibility of rye to leaf rust were carried on in the autumn of 1921 to determine the susceptibility of a number of the principal rye varieties. Fifty-nine selections grown at Arlington Experiment Farm, near Washington, D. C., were obtained. All of these had been grown for two or more years in adjacent rows and, consequently, some crossing probably had taken place. That there still existed considerable individuality in them, however, was shown by the variations in yield observed in the 1921 harvest. Six varieties of winter rye and three of spring rye were obtained from Mr. R. R. Mulvey of the Soils and Crops Department, Purdue University Agricultural Experiment Station. Of these, the Rosen and Wisconsin No 2 varieties had just been obtained from the Michigan and Wisconsin agricultural experiment stations, respectively, where precautions are taken to maintain their purity. The other varieties had been grown in close proximity for several years and doubtless had crossed. Additional pedigreed seed of Rosen rye was obtained from Prof. J. F. Cox, of Michigan Agricultural College, where this variety is maintained in a pure condition. Seed of Abruzzes rye was obtained from Prof. G. M. Garren, of the North Carolina Agricultural Experiment Station, where it is the leading variety and, therefore, probably quite pure.

TABLE II.—*Data on resistance of 70 varieties and selections of rye to leaf rust, Puccinia dispersa, at La Fayette, Ind., in 1922*

Variety.	C. I. No.[a]	Source.	Number of plants inoculated.	Resistant plants.	
				Number.	*Per cent.*
Abruzzes	.....	N. C. Agr. Exp. Sta.	81	7	8.6
Do	.....	Ind. Agr. Exp. Sta.	38	3	7.9
Do	40–1	Cereal Inv.	92	4	4.3
Do	40–2	do	72	5	6.9
Do	40–3	do	84	5	5.9
Do	40–4	do	83	5	6.0
Do	40–5	do	80	3	3.7
Do	40–6	do	72	3	4.2
Do	40–7	do	88	5	5.7
Do	40–8	do	63	1	1.6
Do	[b] 40–47	do	87	4	4.6
Do	[b] 40–48	do	71	7	9.9
Do	[b] 40–49	do	73	3	4.1
Do	[b] 40–55	do	35	7	20.0
Do	[b] 40–56	do	29	3	10.3
Do	[b] 40–57	do	29	6	20.7
Do	[b] 40–59	do	48	7	14.6
Do	[b] 40–61	do	63	4	6.3
Common Spring	.....	Ind. Agr. Exp. Sta.	134	9	6.7
Giant Winter	30–9	Cereal Inv.	57	1	1.8
Do	30–11	do	61	2	3.3
Do	30–12	do	57	1	1.8
Do	30–13	do	91	1	1.1
Do	30–14	do	59	2	3.4
Do	30–15	do	56	3	5.4
Do	30–16	do	38	1	2.6
Do	30–17	do	48	1	2.1

[a] Numbers preceding dash are Office of Cereal Investigations accession numbers; those following dash are row number in the Arlington Experiment Farm nursery at Washington, D. C., in 1921, and represent selections (made in 1918) or strains, in most cases.

[b] Selection made previous to 1918.

TABLE II.—*Data on resistance of 70 varieties and selections of rye to leaf rust, Puccinia dispersa, at La Fayette, Ind., in 1922*—Continued

Variety.	C. I. No.	Source.	Number of plants inoculated.	Resistant plants.	
				Number.	*Per cent.*
Giant Winter	30–18	Cereal Inv.	34	1	2.9
Do	30–19	do	44	3	6.8
Do	30–21	do	50	1	2.0
Do	30–22	do	43	1	2.3
Do	30–23	do	42	1	2.4
Henry	138–25	do	40	1	2.5
Do	138–26	do	47	1	2.1
Do	138–27	do	59	5	8.5
Do	138–28	do	73	1	1.4
Invincible	207–46	do	92	5	5.4
Ivanov	152–29	do	66	1	1.5
Do	152–31	do	64	5	7.8
Do	152–32	do	49	2	4.1
Mammoth Winter		Ind. Agr. Exp. Sta.	63	4	6.3
Mexican	[b] 108–62	Cereal Inv.	51	5	9.8
Petkus		Ind. Agr. Exp. Sta.	63	7	11.1
Prolific Spring		do	151	10	6.6
Rosen		do	59	11	18.6
Do		Mich. Agr. Exp. Sta.	89	16	18.0
Do	[c] 195–45	Cereal Inv.	92	10	10.9
St. John	130–33	do	44	1	2.3
Do	130–43	do	78	4	5.1
Do	[b] 130–63	do	56	7	12.5
Select Spring		Ind. Agr. Exp. Sta.	169	7	4.1
Star		do	76	16	21.0
Virginia	128–24	Cereal Inv.	44	1	2.3
Von Ruemker No. 1	173–37	do	65	4	6.2
Do	173–44	do	82	1	1.2
Do	[b]134–52	do	76	7	9.2
Do	[b]134–53	do	108	5	4.6
Von Ruemker No. 2	174–38	do	60	2	3.3
Do	174–42	do	78	4	5.1
Wisconsin No. 2 (Schlanstedt).		Ind. Agr. Exp. Sta.	77	4	5.2
Unnamed	34	Cereal Inv.	56	6	10.7
Do	[d]39	do	70	6	8.6
Do	[e]41	do	77	5	6.5
Do	[f]132–51	do	85	16	18.8
Do	[b]54	do	33	2	6.1
Do	[b]58	do	54	8	14.8
Do	[c]178–64	do	52	8	15.4
Do	[c]183–65	do	44	1	2.3

[b] Selection made previous to 1918.
[c] Not selections; 178–64 from Taurida, Russia, S. P. I. No. 38692; 183–65 an unnamed lot of seed from Utah.
[d] Selection made at Cobleskill, N. Y., 1918.
[e] Selection made in Tennessee, 1918.
[f] Selection made at Cornell University, Ithaca, N. Y., in 1912.

These varieties and strains were tested by sowing a number of pots of each, about 10 kernels being sown to a pot. When the seedlings were in about the second or third leaf, they were inoculated with a culture of leaf rust obtained from volunteer rye at La Fayette, Ind., and maintained in the greenhouse as stock material. Infection appeared in from 7 to 10 days and when the rust had reached its maximum development, usually about 2 weeks after inoculation, notes were taken. Table II

shows the results obtained. Plants showing types of infection 0, 1, and 2 are listed as resistant. A few of the more highly resistant plants of a number of the varieties and strains were transplanted to larger pots and grown to maturity, being crossed and selfed to obtain material for further work.

An examination of Table II shows that one or more resistant plants were found in each of the varieties and selections. Considerable variation apparently exists as to the number of resistant individuals to be found in these varieties and selections. This may be due in some cases to the relatively small number of plants which it was possible to study. The differences between such varieties and selections as Rosen, Abruzzes 40–55, 40–56, 40–59, 40–48, and Star on the one hand, and Giant Winter, Henry, and Virginia on the other, probably represent varietal differences in the occurrence of resistant strains. It may be that a number of the strains of the latter varieties, when in the pure condition, are entirely susceptible, the small degree of resistance shown coming from cross fertilization with adjacent more highly resistant strains. It is, however, significant that such varieties as Rosen from Michigan, Abruzzes from North Carolina, and the spring ryes from Purdue University, all fairly pure varieties, show resistance. The data indicate that to some extent resistance is to be expected in all the varieties of rye now commonly grown.

DISCUSSION

The discovery of rye individuals resistant to leaf rust of rye is of considerable interest because of the lack of data or observations on disease resistance in this cereal. Although 68 selections of rye representing about 17 of the principal varieties grown in this country were studied, no variety was found which was uniformly resistant. As rye is almost always cross-pollinated, this would be expected unless a variety was selected with rust resistance in view. On the other hand, all the selections studied showed at least a few resistant individuals. This indicates, at least in all the varieties studied and probably in others as well, that the factor or factors determining resistance have not been eliminated by the processes which selected varieties from the original parental stock. Rye varieties have been obtained largely by repeated selection of desirable types without precautions being taken to prevent cross pollination. As a result, the varieties are relatively few and ill-defined, differing mostly in ability to develop and yield well, and composed of many strains, at least so far as disease resistance is concerned. The differences shown between the various selections and varieties as to proportion of resistant individuals may be due to a difference in the number of the susceptible and resistant strains of which they may be considered to be constituted. The constant crossing and recrossing which must occur among these strains doubtless cause the number of resistant individuals to vary considerably, so that any one test is probably only a rough estimate. Before the exact degree of resistance in the varieties can be determined, it doubtless will be necessary to establish, if possible, a number of pure lines by repeated selfing and selection similar to the methods being employed with corn in this country.

The data obtained are insufficient to justify drawing conclusions as to inheritance in rye of resistance to leaf rust. It is obvious that a number of generations of breeding will be necessary before the genetic constitution of material of such complexity can be known with any degree

of accuracy. The results obtained by crossing the two plants, 8 and 9, resistant to leaf rust, however, are suggestive. The appearance of two highly susceptible and seven susceptible plants in the progeny from this cross strongly indicates that resistance is dominant. The appearance of so many different types in the offspring is confusing. Whether more than one pair of factors is involved, or one main pair with modifying factors, as Puttick (*10*) has suggested as an explanation for the appearance of different types of susceptibility to *Puccinia graminis* in segregates from a Marquis-Mindum wheat cross, or whether we have a number of segregating strains of rye which in homozygous condition may differ in respect to type of susceptibility, must be determined by future study. It is evident, however, that the problem of obtaining rust-resistant strains of rye is complicated not only by the high degree of self sterility and the consequent slow progress which can be made by selfing, but also by the dominance, as seems probable, of the desired quality of resistance and the consequent longer process of breeding before it is certain that a pure homozygous strain has been obtained.

SUMMARY

(1) Rye plants have been found which show high resistance to and in some cases practically complete immunity from the leaf rust of rye, *Puccinia dispersa* Erikss.

(2) Sixty-eight selections and varieties of rye, including such varieties as Abruzzes, Giant Winter, Henry, Invincible, Ivanov, Mammoth Winter, Mexican, Petkus, Rosen, St. John, Star, Von Ruemker, Wisconsin No. 2 (Schlanstedt selection), and a number of unnamed introductions, were studied as to susceptibility to leaf rust.

(3) None of these varieties or selections was uniformly resistant.

(4) All of these varieties or selections showed at least a few individuals having high resistance.

(5) Crosses made by bagging heads of two highly resistant plants together showed gradation in the susceptibility of the plants produced, varying from high susceptibility through intermediate grades of resistance to complete immunity.

(6) The production of susceptible individuals from a cross between resistant ones indicates that resistance probably is dominant. The production of intermediate types, however, would indicate complicating factors.

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PLATE 1

Types of susceptibility shown by rye plants to leaf rust, *Puccinia dispersa*. All natural size.

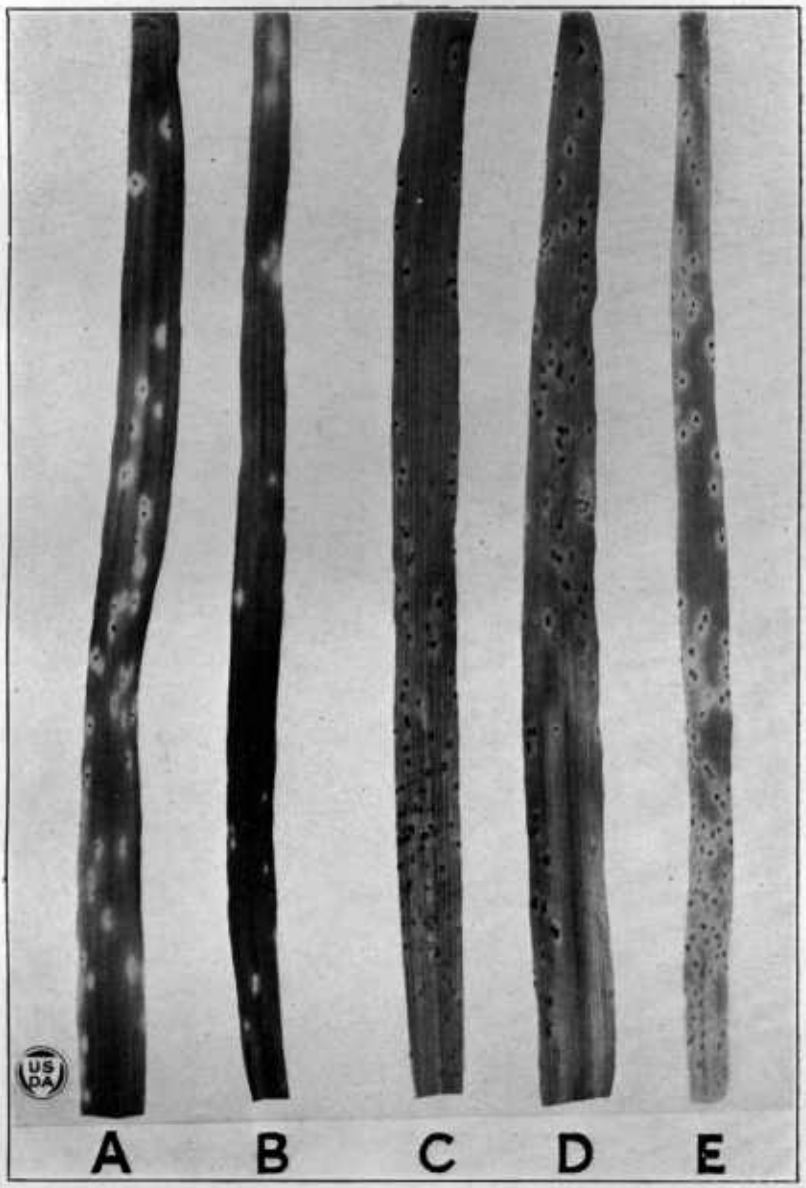
A.—Leaf showing the resistance of rye plant 9. Note the hypersensitive areas and the small uredinia.

B.—Leaf showing the high resistance of rye plant 8. Note the few hypersensitive areas and lack of uredinia.

C.—Leaf showing the susceptibility of rye plant 7. Note the large uredinia and lack of hypersensitiveness.

D.—Leaf showing the susceptibility of rye plant 10. Note the large uredinia and lack of hypersensitiveness.

E.—Leaf showing the moderate resistance of rye plant 11. Note the hypersensitive areas and the large uredinia accompanying each.


A
B
C
D
E

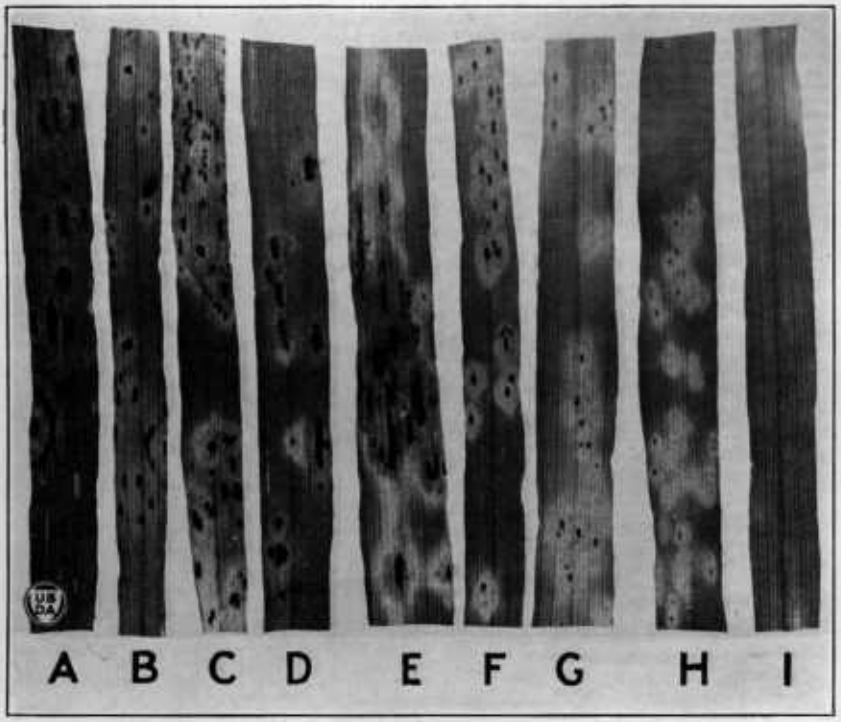

A B C D E F G H I

PLATE 2

Types of susceptibility shown by offspring of selfs and crosses between rye plants 7, 8, 9, and 10 to leaf rust of rye, *Puccinia dispersa*. X2.

A.—Uredinia very large, often circular. Type 4.

B.—Uredinia midsized, less often circular. Type 3.

C.—Uredinia midsized, infected areas somewhat chlorotic. Type 3.

D.—Uredinia midsized or large, sometimes accompanied by definite hypersensitive spots. Type X.

E.—Uredinia midsized or large, infected areas green, bordered by chlorotic tissue. Type 4.

F.—Uredinia midsized in large, definite hypersensitive spots. Type 2.

G.—Uredinia small in less definite hypersensitive spots, the latter sometimes without uredinia. Type 1.

H.—Hypersensitive areas abundant, only occasionally containing small uredinia. Type 1.

I.—Hypersensitive areas few, indefinite, no uredinia produced. Type 0.