PHYSIOLOGIC SPECIALIZATION OF MELAMPSORA LINI ON LINUM USITATISSIMUM [1]

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INTRODUCTION

Melampsora lini (Pers.) Lév., the fungus that causes rust of cultivated flax, *Linum usitatissimum* L., occurs in all the major seed flax- and fiber-flax-producing areas of the world. Injury to the seed crop results from a reduction in the amount of foliage and from the utilization by the fungus of some of the food of the host plant. In addition to interfering with the normal photosynthetic metabolism of the host plant, rust on fiber flax injures the quality by causing breakage of fibers and preventing normal retting, thus producing what is known as "measly" fibers (*23*).[3] Consequently a small amount of infection may injure the quality of a fiber-flax crop, while it is only under epidemic conditions that the rust may be destructive to seed flax. Only occasionally is flax rust very destructive in Minnesota and the Dakotas, where most of the domestic flaxseed is grown. However, it sometimes occurs in epidemic form in these areas, and Brentzel [4] and Hart (*9*) have reported losses ranging from a trace to 100 percent.

Measures that have been recommended for the control of flax rust include early sowing, thorough cleaning of the seed, crop rotation, use of high, well-drained land, destruction or removal of infected straw, and the use of resistant varieties. Henry (*10*) considered the last-named method the most promising and found rust immunity to be inherited independently of morphologic type or wilt resistance.

In a program to develop disease-resistant varieties of crop plants it is essential to know whether more than one physiologic form of the pathogen occurs and, if so, the varietal host range, distribution, and stability of each form. The object of the investigation herein reported was to obtain this information in regard to *Melampsora lini*.

HISTORICAL REVIEW

Persoon (*18*) described a rust fungus on *Linum catharticum* L. and *L. usitatissimum* in 1801 and named it *Uredo miniata β lini*. In 1847 Léveillé (*15*) transferred it to the genus *Melampsora*, calling it *M. lini*. Buchheim (*5*) states that Körnicke, in 1865, decided that the rust on cultivated flax, *L. usitatissimum*, was physiologically

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[3] Reference is made by number (italic) to Literature Cited, p. 836.

[4] FROMME, F. D. RUST CAUSED BY MELAMPSORA LINI (PERS.) DESM. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bull. Sup. 15: 168–169, illus. 1921. [Mimeographed.]

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distinct from that on *L. catharticum*, and called the former *M. lini* var. *liniperda*. Since then the host range of rusts occurring on different species of *Linum* has been studied by a number of investigators. Fuckel (*8*), Palm (*17*), and Buchheim (*5*) concluded from cross-inoculation studies that rust on cultivated flax was physiologically and, in some cases, morphologically distinct from that on certain wild flaxes. Arthur (*2*), in demonstrating that *M. lini* was eu-autoecious, obtained pycnia and aecia on *L. lewisii* Pursh and *L. usitatissimum* by inoculation with teliospores produced on the latter species. Hart (*9*) was unable, however, to infect *L. lewisii* with urediospores from *L. usitatissimum* but did secure successful infection of *L. rigidum* Pursh. Lafferty, Rhynehart, and Pethybridge (*14*) obtained slight but abnormal infection of *L. angustifolium* Huds. with urediospores from *L. usitatissimum*. Henry (*11*) found that certain strains of *L. usitatissimum*, *L. angustifolium*, *L. usitatissimum* var. *crepitans* Bönningh., *L. rigidum*, and *L. sulcatum* Riddell were completely susceptible to *M. lini* collected on *L. usitatissimum*, and that certain strains of *L. usitatissimum* and *L. angustifolium*, as well as all tested strains of *L. perenne* L., *L. austriacum* L., *L. grandiflorum* Desf., *L. flavum* L., and *L. catharticum*, were immune.

Hart (*9*) obtained urediospore collections of *Melampsora lini* on *Linum usitatissimum* from a number of localities in the United States and Canada but could not demonstrate the occurrence of physiologic forms from their reactions on a susceptible and an immune variety of cultivated flax. Henry (*10*) suspected the occurrence of physiologic forms of rust on cultivated flax but did not demonstrate their existence. He found that four strains of flax that had been selected by Dorst (*7*) for their resistance to rust in the Netherlands were uniformly susceptible when grown in Minnesota.

MATERIAL AND METHODS

RUST COLLECTIONS AND INOCULATION PROCEDURE

The rust collections used in these studies were made in the field in 1931, 1932, 1933, and 1934. Because of drought, rust was of little economic importance during this period in the flaxseed-producing area of the United States, but a scattered infection occurred throughout Minnesota and the eastern parts of North Dakota and South Dakota. The pathogenicity of 99 uredial collections was studied during these 4 years. Most of the field collections contained but a few uredia and each collection was increased on a susceptible variety in the greenhouse. The urediospores thus obtained were collected in glass vials and stored at 4° C., at which temperature they retained their viability from 2 to 4 months. Pathogenicity tests were made by inoculating approximately twelve 30-day-old plants of each variety with the increased supply of urediospores by dusting the spores from a camel's-hair brush onto the leaves and terminal bud. The inoculated plants were placed in moist chambers for 24 hours at a temperature of 14° to 16° C. and sprayed periodically with an atomizer. They were then removed to rust compartments in a greenhouse kept at a temperature of approximately 20° C. During the winter months a light day of 16 hours was maintained by supplementing daylight with artificial illumination. Final readings were made 10 to 15 days after inoculation, depending on the effect on pustule formation of temperature and light conditions during the period of incubation.

DIFFERENTIAL HOSTS

Although the existence of physiologic forms of *Melampsora lini* on common flax had been suspected by Henry (*10*) prior to the present studies, it had not been proved nor had suitable differential hosts been discovered. The work of previous investigators on physiologic specialization in the rusts and other fungi had indicated that differential hosts most likely would be obtained from resistant varieties and those possessing diverse morphologic characters. In trying to discover potential differentials, the reaction of 50 varieties of flax to the 36 rust collections made in 1931 and 1932 was studied. These varieties had been chosen because they represented diverse morphologic types or had been reported as resistant to rust.

In these tests it was discovered that many varieties reported as resistant in field trials showed no resistance in greenhouse inoculation tests. Furthermore, the reaction of individual plants of varieties possessing some resistance was extremely variable. Consequently, it was necessary to develop lines pure for rust reaction from those varieties that gave indications of possessing differential potentialities. This was accomplished by plant selection. It was found, for example, that two-thirds of the plants of Williston Golden (C. I.[5] 25) showed a high degree of resistance when inoculated with form 1, and that the remaining third showed extreme susceptibility. All plants of this variety were susceptible to form 2. Those plants that showed resistance to form 1 were grown to maturity in the greenhouse, and seed from each plant was increased in the field nursery. The progeny of each plant selection was harvested separately and tested for rust reaction to form 1. Many of the progenies thus obtained continued to segregate for resistance and susceptibility, but several were found to be pure for resistance. One of the latter was subsequently selected as a differential strain for future work. Similarly, it was found that 90 percent of the plants of Buda (C. I. 270) were resistant to form 1, while all plants of this variety were susceptible to form 4. A strain of this variety that was pure for resistance to form 1 was developed by the method used in obtaining the resistant strain of Williston Golden.

The reaction of the differential strains of Williston Golden and Buda to the 36 collections made in 1931 and 1932 indicated that at least 5 physiologic forms of flax rust were present. Monosporous uredial cultures were obtained from each of the 5 forms that appeared to be physiologically distinct. In every instance the pathogenicity of the monosporous culture was identical with that of the original collection. The pathogenicity of these 5 monosporously derived forms to 115 additional varieties was determined in 1932. By these tests and the subsequent increase of certain plant selections, a line pure for rust reaction was obtained from each of 12 additional varieties of flax possessing differential potentialities. Four of these, Samarkan (C. I. 514), Abyssinian (C. I. 511), and Akmolinsk (C. I. 515 and 520), although varying somewhat in the degree of susceptibility, reacted similarly to the different forms. Another strain of Abyssinian (C. I. 701) was resistant to the same forms as were the varieties mentioned above but was also resistant to some of the rust forms to which these varieties were susceptible. Selections from Redwing (C. I. 499) possessed varying degrees of resistance but reacted in general as did the differential strain from Buda. The selection from the fiber flax, J. W. S.

[5] C. I. refers to accession number of the Division of Cereal Crops and Diseases.

(C. I. 708), was either highly resistant or very susceptible to the different forms. The selection from Argentine (C. I. 705) was particularly sensitive to changes in light conditions. This change in reaction was especially noticeable in those forms to which this selection was more or less resistant. The number and size of pustules and the abundance of spores in the pustules were greater in clear weather than in cloudy weather. However, the change in reaction was not sufficient to nullify the value of this variety as a differential. The selections from Diadem (C. I. 321), "very pale blue crimped" (C. I. 647), and Williston Brown (C. I. 803), a brown-seeded selection, probably a hybrid or a mixture, found in a sample of Williston Golden (C. I. 25), were susceptible to most forms of rust but were sufficiently resistant to other forms to be of value as differentials. The selection from Kenya (C. I. 709) was resistant to most forms but semiresistant to some.

HOST REACTION AND TYPES OF INFECTION

The classes of host reaction and infection types used by Stakman and Levine (*20*) served as a guide for formulating the classification used in these studies. Apparently, flax varieties give more diverse manifestations of resistance to rust infection than do wheat varieties, and the classification of host reaction was modified accordingly. The principal types of reaction of flax varieties to rust infection are described below and shown in plate 1.

Classes of host reaction		*Types of rust infection*
Nearly immune	(0)	No uredia developed; hypersensitive flecks or necrotic lesions usually present, but sometimes there is no evidence of infection.
Resistant	(1)	Uredia minute to small, rarely extending through the leaf, usually distinct and scattered in chlorotic to necrotic areas, but in some cases pustule formation is not accompanied by either chlorosis or necrosis of the surrounding leaf tissue.
	(2)	Uredia small to medium, associated with distinct necrosis of the leaf; may be scattered or may form crustlike aggregations in necrotic areas; if isolated, usually are surrounded by a necrotic zone.
Semiresistant	(3−)	Uredia variable; heavily inoculated areas necrotic, with arrested pustule development; medium to large pustules produced in healthy tissue adjacent to necrotic areas; pustules on stem and cotyledons small but with no evidence of hypersensitiveness.
Moderately susceptible	(3)	Uredia medium to large; well developed but not compound; usually extending through the leaf to both surfaces; development somewhat retarded in heavily infected portions of the leaves; tissues adjacent to uredia may become more or less chlorotic as the pustules mature.
Highly susceptible	(4)	Uredia large and, if isolated, usually compound, extending through leaf to both surfaces; at first leaves show little chlorosis but later may become chlorotic and die prematurely.

Hard and fast rules for pustule classification cannot be followed. The types of infection exhibited by a variety depend upon such factors as light intensity, length of day, temperature, and age and vigor of the host plant, as well as upon the pathogenic properties of the rust form involved. All ranges of reaction between immunity and complete susceptibility occur, and whether the borderline cases fall into one type of host reaction or into another often depends upon the arbitrary judgment of the observer.

There appear to be at least two distinct forms of resistance in flax. In some varieties resistance is manifested by a reduction in the size of the individual uredia, together with more or less chlorosis, and the eventual premature death of the infected areas of the leaf. In other varieties resistance is manifested by necrosis of the infected region, coupled with more or less repressed pustule formation. Varieties with host reactions of type 1 show different degrees of the first form of resistance; those with reactions of type 2, different degrees of the second form. The extreme cases of both kinds of resistance would fall in the group having reactions of type 0, in which chlorosis or necrosis of the infected portions of the leaves occurs without pustule formation. Reactions of type 1— include those in which chlorosis of the infected leaves occurs but in which the minute uredia do not break through the epidermis; reactions of type 1 include those in which the small uredia, usually borne in chlorotic areas of the leaves, break through the epidermis; and reactions of type 1+ include those in which small, erumpent uredia are produced, with but slight, if any, chlorosis of the surrounding leaf tissue. Reactions of type 2— are characterized by the production of small aggregations of rudimentary uredia in necrotic areas of the leaves; those of type 2, by the production of small to mid-sized uredia surrounded by a sharp necrotic zone; and those of type 2+, by a crustlike structure resulting from the aggregation of uredia produced in necrotic areas of the leaf. Each form of resistance, as represented by types 1 and 2, covers a range of host reaction extending from near immunity to the borderline of susceptibility. Consequently, one form parallels the other in degree of resistance and neither can be considered, in this respect, subordinate to the other.

No cases of a truly mesothetic type of rust infection, comparable to those occurring in wheat (*20*), oats (*3*), and rye (*6*), were observed on flax. However, there were cases on the borderline of resistance and susceptibility in which monosporous rust cultures produced both necrosis and normal uredia. Since these uredia were well developed and not always produced in or surrounded by necrotic areas, infections of this type were classified as the 3— type and the varietal reaction as semiresistant.

EXPERIMENTAL RESULTS

DIFFERENTIATION OF PHYSIOLOGIC FORMS

Fourteen physiologic forms of *Melampsora lini* infecting *Linum usitatissimum* have been differentiated by the use of seven varieties of cultivated flax. With the study of additional rust collections and the discovery and purification of still other differential varieties, it is probable that more forms will be distinguished. Tests already conducted indicated that additional forms may have been present in the 99 rust collections studied. It was thought inadvisable, however, to establish new forms based on these minor differences, even though they were consistently obtained.

These 14 physiologic forms have been differentiated by the reaction of the selected strain from each of the seven varieties used in the following key. The reactions of each of these seven varieties are given in table 1. In this table the reactions of two additional varieties also are given for additional information and for possible use in differentiating forms not yet studied.

KEY

- Buda resistant.
  - Williston Golden resistant.
    - Akmolinsk resistant.
      - Williston Brown semiresistant to resistant .... Form 10
      - Williston Brown susceptible .... Form 1
    - Akmolinsk susceptible.
      - J. W. S. resistant .... Form 5
      - J. W. S. susceptible .... Form 7
  - Williston Golden susceptible.
    - "Very pale blue crimped" resistant .... Form 11
    - "Very pale blue crimped" susceptible .... Form 6
- Buda semiresistant.
  - Williston Golden resistant .... Form 3
  - Williston Golden susceptible .... Form 14
- Buda susceptible.
  - Williston Golden resistant.
    - Akmolinsk resistant.
      - J. W. S. resistant.
        - Kenya resistant .... Form 4
        - Kenya semiresistant .... Form 12
      - J. W. S. susceptible .... Form 13
    - Akmolinsk susceptible .... Form 8
  - Williston Golden susceptible.
    - J. W. S. resistant .... Form 2
    - J. W. S. susceptible .... Form 9

TABLE 1.—*Reactions of pure-line selections from 9 differential varieties of Linum usitatissimum to 14 physiologic forms of Melampsora lini as determined in greenhouse tests at Fargo, N. Dak., 1935* [1]

Physiologic form	Types of rust infection and reactions of differential hosts								
	Buda (C. I. 270)			Williston Golden (C. I. 25)			Williston Brown (C. I. 803)		
	Infection type: Range	Infection type: Predominant	Host reaction	Infection type: Range	Infection type: Predominant	Host reaction	Infection type: Range	Infection type: Predominant	Host reaction
1	0 to 1+ [1]	1−	R+	0 to 1	1	R+	3	3	S
2	1 to 3	3	S−	3 to 4	3	S+	3− to 3	3	S
3	1− to 3−	3−	SR	1− to 1	1	R+	3− to 3	3	S
4	3 to 4	3	S+	1− to 1	1	R+	3	3	S
5	0 to 1−	0	R+	1 to 1+	1+	R−	3	3	S
6	1− to 1	1	R+	3 to 4	3	S+	3	3	S
7	1 to 1+	1	R+	1− to 1	1	R+	3− to 3	3−	S−
8	3	3	S	1− to 1	1	R+	3	3	S
6	1+ to 3	3	S−	1+ to 3	3	S−	3	3	S
10	0	0	I	0 to 1	0	R+	1 to 3−	2	SR
11	0 to 1−	0	R+	3 to 4	3	S+	3	3	S
12	1 to 3	3	S−	1 to 1+	1	R	3	3	S
13	1+ to 3	3	S−	1 to 1+	1+	R−	3	3	S
14	1 to 3−	3−	SR	3	3	S	3	3	S

[1] Plus and minus signs indicate somewhat greater or lesser amount of rust than the nearest figure representing the infection type, and the letters signify the following: R, resistant; S, susceptible; SR, semiresistant; and I, immune.

EXPLANATORY LEGEND FOR PLATE 1

Infection types produced by *Melampsora lini* on selected varieties of cultivated flax, *Linum usitatissimum*.

A, Type 0. No uredia produced, but chlorotic to necrotic areas formed in inoculated portions of the leaves. Akmolinsk, C. I. 515, inoculated with form 4.

B, Type 1. Small uredia formed usually in association with chlorosis of the surrounding leaf tissue. Williston Golden, C. I. 25, inoculated with form 1.

C, Type 2. Small to medium uredia of subnormal development surrounded by sharply defined necrotic areas. Williston Brown, C. I. 803, inoculated with form 10.

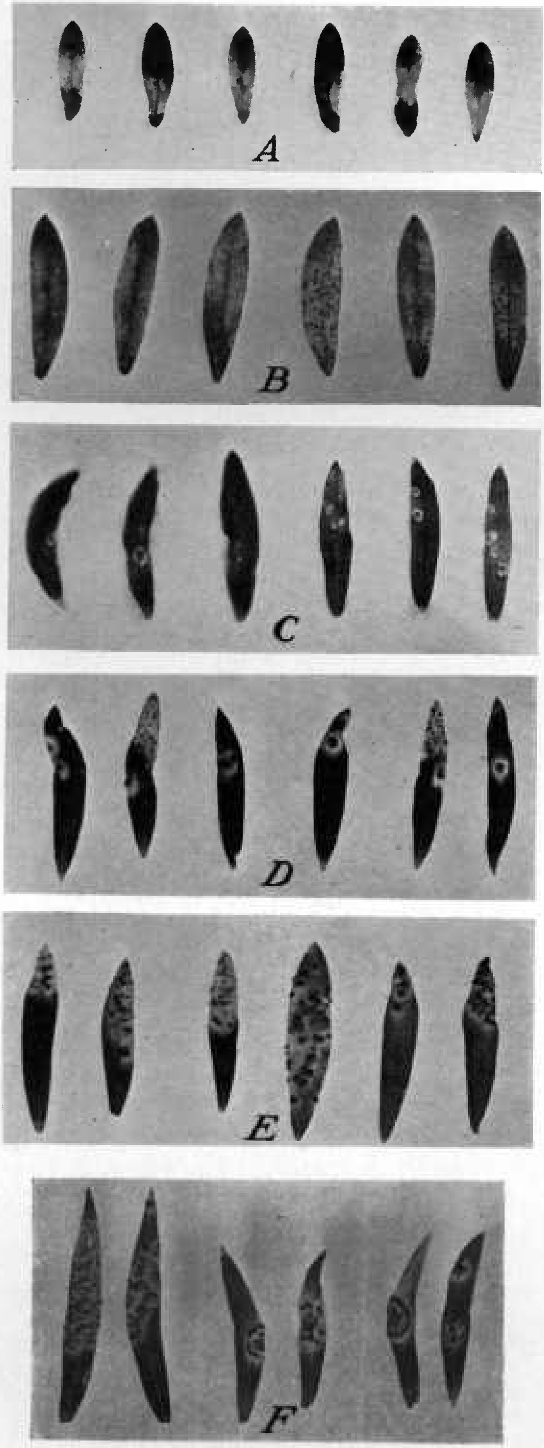
D, Type 3−. Isolated uredia, large and well developed but not compound, surrounded by a chlorotic area which may become necrotic; heavily infected portions of the leaves are chlorotic with arrested uredial development. Buda, C. I. 270, inoculated with form 3.

E, Type 3. Uredia large and well developed but not compound; considerable chlorosis in heavily infected areas, but uredial development only slightly retarded. Williston Golden, C. I. 25, inoculated with form 2.

F, Type 4. Uredia large and, if isolated, compound with but slight chlorosis except in the older infections. Bison, C. I. 389, inoculated with form 2.

A to *E*, × 1.5; *F*, natural size.

PLATE 1



FOR EXPLANATORY LEGEND SEE OPPOSITE PAGE.

TABLE 1.—*Reactions of pure-line selections from 9 differential varieties of Linum usitatissimum to 14 physiologic forms of Melampsora lini as determined in greenhouse tests at Fargo, N. Dak., 1935*—Continued.

Physiologic form	Types of rust infection and reactions of differential hosts								
	Akmolinsk (C. I. 515)			J. W. S. (C. I. 708)			"Very pale blue crimped" (C. I. 647)		
	Infection type		Host reaction	Infection type		Host reaction	Infection type		Host reaction
	Range	Predominant		Range	Predominant		Range	Predominant	
1	0 to 1−	0	R+	0	0	I	3− to 3	3	S
2	0 to 1−	0	R+	0	0	I	3− to 3	3	S
3	3 to 4	3	S+	0	0	I	3− to 3	3	S
4	0 to 1	1−	R+	0	0	I	3− to 3	3	S
5	3 to 4	3	S+	0	0	I	1 to 3−	3−	SR
6	0 to 1	1−	R+	0	0	I	3− to 3	3	S
7	3 to 4	3	S+	3	3	S	2 to 3	3	S−
8	3 to 4	3	S+	0	0	I	3	3	S
9	0	0	I	3 to 4	3	S+	3	3	S
10	0	0	I	0	0	I	3− to 3	3	S
11	0 to 1	1−	R+	0	0	I	0	0	I
12	0 to 1−	0	R+	0	0	I	3− to 3	3	S
13	0	0	I	3 to 4	3	S+	3− to 3	3	S
14	0	0	I	0	0	I	2 to 3	3	S−

Physiologic form	Types of rust infection and reactions of differential hosts								
	Kenya (C. I. 709)			Argentine (C. I. 705)			Abyssinian (C. I. 701)		
	Infection type		Host reaction	Infection type		Host reaction	Infection type		Host reaction
	Range	Predominant		Range	Predominant		Range	Predominant	
1	0 to 1	1−	R+	1− to 3−	2+	SR	0	0	I
2	1 to 2	2	R+	2 to 3−	2+	SR	0	0	I
3	2+ to 3−	2+	SR	1− to 3−	2+	SR	1	1	R+
4	2− to 2+	2−	R	2 to 3−	2+	SR	0	0	I
5	0 to 2	0	R+	2 to 3−	2+	SR	1 to 1+	1	R+
6	0 to 2+	2−	R	2 to 3−	2+	SR	0	0	I
7	0 to 2−	2−	R+	3− to 3	3	S	1 to 1+	1	R+
8	2 to 3−	2+	SR	2 to 3−	2+	SR	3	3	S
9	2− to 2+	2−	R	2+ to 3−	2+	SR	0	0	I
10	0 to 1−	0	R+	0 to 1	0	R+	0	0	I
11	0	0	I	2 to 3−	2+	SR	0	0	I
12	2+ to 3−	2+	SR	2+ to 3−	2+	SR	0	0	I
13	2+ to 3−	2+	SR	2+ to 3−	2+	SR	0	0	I
14	0 to 2−	2−	R+	0 to 2+	2	R	0	0	I

DESCRIPTION OF FORMS

Form 1.—Differential selections of J. W. S. and Abyssinian C. I. 701 nearly immune; Buda, Williston Golden, Akmolinsk, and Kenya highly resistant; Argentine C. I. 705 semiresistant; Williston Brown susceptible. Under optimum rust conditions, Williston Golden developed infection types 1 to 1+; under suboptimum conditions it showed pronounced chlorosis and subsequent necrosis of inoculated leaf areas and an occasional pustule of type 1− to 1. Typical response of Buda, Akmolinsk, and Kenya, formation of chlorotic to necrotic areas with an occasional pustule of type 1−. Response of Argentine C. I. 705 variable; uredia usually aggregated in necrotic areas; under suboptimum rust conditions uredia dry prematurely and spore production is sparse; under optimum rust conditions uredia well developed and sporulation abundant.

Form 2.—Buda susceptible; Williston Golden very susceptible, and J. W. S. nearly immune. Uredia on Buda medium in size, numerous, sporulation abundant; stems and cotyledons show no resistant reaction; heavily infected leaves become chlorotic and prematurely dry.

Form 3.—Buda semiresistant; Williston Golden highly resistant; Akmolinsk very susceptible; Kenya semiresistant. Buda, uredia type 3—; variable, heavily inoculated areas necrotic with arrested pustule development, normal uredia in adjacent tissue; uredia on stem and cotyledons small but otherwise normal.

Form 4.—Buda very susceptible; Williston Golden and Akmolinsk highly resistant; Kenya resistant; J. W. S. nearly immune. Infection on Buda normal, uredia large, rarely compound, sporulation abundant, but under suboptimum conditions Buda less susceptible to form 4 than Akmolinsk to form 3 or Williston Golden to form 2. Kenya, heavily inoculated areas chlorotic to necrotic, pustules rudimentary, usually in necrotic areas at leaf margins.

Form 5.—Resistance of Buda and Kenya differentiates this form from form 3. Williston Golden slightly more susceptible than to form 3; Akmolinsk very susceptible; and J. W. S. nearly immune from both forms.

Form 6.—Buda highly resistant; Williston Golden very susceptible. Susceptibility of the "very pale blue crimped" (C. I. 647) differentiates this form from form 11.

Form 7.—Buda, Williston Golden, and Kenya very resistant; Akmolinsk very susceptible; and J. W. S. susceptible; Williston Brown semiresistant to moderately susceptible, uredia large, fewer than normal, and surrounding tissue dries prematurely. The only form producing a susceptible reaction on Argentine C. I. 705 under suboptimum conditions.

Form 8.—J. W. S. nearly immune; Williston Golden highly resistant; Buda susceptible; and Akmolinsk very susceptible. The only form that produces a susceptible reaction on Abyssinian C. I. 701.

Form 9.—Susceptibility of J. W. S. differentiates this form from form 2; Williston Golden appreciably less susceptible than to form 2.

Form 10.—Apparently the least virulent of all forms. Under suboptimum conditions Williston Brown resistant; under optimum conditions semiresistant. Buda, Williston Golden, Akmolinsk, and Kenya slightly more resistant than to form 1; Argentine C. I. 705 much more resistant.

Form 11.—The immunity of the "very pale blue crimped" (C. I. 647) differentiates this form from form 6. This is the only form to which this variety is highly resistant.

Form 12.—Kenya semiresistant, uredia large, well developed, aggregated in the heavily inoculated regions that become chlorotic and tend to dry up prematurely; Buda susceptible; Williston Golden resistant; Akmolinsk highly resistant; J. W. S. nearly immune. Differentiated from form 4 by the more susceptible reaction of Kenya and the less susceptible reaction of Buda.

Form 13.—Susceptibility of J. W. S. differentiates this form from forms 4 and 12.

Form 14.—Buda semiresistant; Williston Golden susceptible; Akmolinsk, J. W. S., and Abyssinian C. I. 701 nearly immune; Argentine C. I. 705 resistant; and Kenya very resistant. Differentiated from form 2 by semiresistance of Buda and the somewhat less susceptibility of Williston Golden.

GEOGRAPHIC DISTRIBUTION

The localities from which the 99 rust collections were obtained are shown in table 2. More than one form was obtained from several of the collections made in 1934, so that a total of 105 form identifications were made. The distribution of these forms, according to years and States or Provinces in which each was collected, is also shown in table 2.

Physiologic forms 1 to 7, inclusive, were differentiated on the reaction of three differential varieties, Buda, Williston Golden, and Akmolinsk. Since only the type specimen of each of these 7 forms was available for tests with the additional differentials used in the 1934 trials, it is possible that some of the earlier form identifications were not exact. For instance, form 9, which is distinguished from form 2 by the reaction of J. W. S., would have been classified as form 2 prior to the use of J. W. S. as a differential in 1934. Likewise, collections having pathogenic properties of form 10 would have been classed as form 1; and collections having the reactions of forms 12 and 13, as form 4.

Table 2.—*Geographic distribution of physiologic forms of Melampsora lini and number of times each form was isolated from Linum usitatissimum, 1931–34*

Year	Place collected [1]: State or Province	Place collected [1]: Locality	Number of isolates of physiologic form—: 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total number: Isolates	Total number: Forms
1931	Manitoba, Canada	St. Adolphe [2]	1														1	1
		Winnipeg [2]				2											2	1
		Total	1			2											3	2
	North Dakota	Cooperstown	1														1	1
		Fargo				2											2	1
		Hamilton		1													1	1
		Langdon	1		1	1											3	3
		Mandan		1													1	1
		New Salem	1														1	1
		Wishek	1			1											2	2
		Total	4	2	1	4											11	4
	Total		5	2	1	6											14	4
1932	Minnesota	Cooncreek [3]		2		1											3	2
		Lamberton	1														1	1
		Morris				1											1	1
		Northfield		1													1	1
		St. Paul			1												1	1
		Tyler	1														1	1
		Waseca															1	1
		Willmar			1												1	1
		Total	2	3	3	2											10	4
	North Dakota	Carrington			1												1	1
		Cavalier	1														1	1
		Cooperstown			1		1										2	2
		Grafton		1													1	1
		Hurdsfield	1	1													2	2
		Langdon		1													1	1
		Lawton				1											1	1
		Mandan				2											2	1
		Valley City	1														1	1
		Total	3	3	2	3	1										12	5
	South Dakota	Watertown			1												1	1
	Total		5	6	6	5	1										23	5

[1] Unless stated otherwise, collections were made by H. H. Flor. [2] 1 collection was made by F. J. Greaney. [3] 1 collection of physiologic form 2 was made by C. C. Allison.

TABLE 2.—*Geographic distribution of physiologic forms of Melampsora lini and number of times each form was isolated from Linum usitatissium, 1931–34*—Continued

Year	Place collected: State or Province	Place collected: Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total number: Isolates	Total number: Forms
1933	Minnesota	Alexandria			1												1	1
		Cooncreek					1										1	1
		Crookston		1	1												2	2
		Fergus Falls						1									1	1
		Melrose		1													1	1
		Osakis	1														1	1
		Total	1	2	2		1	1									7	5
	North Dakota	Cavalier				1											1	1
		Fargo	2	2		1											5	3
		Finley	1	2													3	2
		Grafton					1										1	1
		Grand Forks					1										1	1
		Lakota				2											2	1
		Langdon		1													1	1
		Minto			1												1	1
		Pekin					1										1	1
		St. Thomas					1										1	1
		Total	3	5	1	4	4										17	5
	Oregon	Astoria [4]							1								1	1
	Total		4	7	3	4	5	1	1								25	7

1934	Minnesota	Ada														2	2	1
		Alexandria	2														2	1
		Averill	1														1	1
		Borup				1											1	1
		Brandon					1				1						2	2
		Breckenridge		1			1										2	2
		Cooncreek [3]											1				1	1
		Crookston	2			1											3	2
		Eldred					1							1	1		3	3
		Fergus Falls														3	3	1
		Northcote [5]		1	1												2	2
		Owatonna						1						1			2	2
		Waseca		1			1										2	2
		Windom	1		1							1					3	3
		Total	6	3	2	2	4	1			1	1	1	2	1	5	29	12
	North Dakota	Argusville					1										1	1
		Casselton														1	1	1
		Fargo	2											1		1	4	3
		Hillsboro		1	1		1				1			1			5	5
		Leonard														2	2	1
		Total	2	1	1		2				1			2		4	13	7
	Oregon	Corvallis [4]								1							1	1
	Total		8	4	3	2	6	1		1	2	1	1	4	1	9	43	13
1931–34	Manitoba		1			2											3	2
	Minnesota		9	8	7	4	5	2			1	1	1	2	1	5	46	12
	North Dakota		12	11	5	11	7				1			2		4	53	8
	Oregon								1	1							2	2
	South Dakota				1												1	1
	Grand total		22	19	13	17	12	2	1	1	2	1	1	4	1	9	105	14

[3] 1 collection of physiologic form 2 was made by C. C. Allison.
[4] Collected by B. B. Robinson.
[5] Physiologic forms 2 and 3 were collected by C. C. Allison.

A number of physiologic forms of flax rust are widely disseminated throughout the flaxseed-producing area of Minnesota, North Dakota, South Dakota, and Manitoba. Forms 1, 2, and 4 apparently were most prevalent during this 4-year period, but the limited number of collections studied scarcely warrants drawing definite conclusions concerning the relative prevalence of the different forms. Apparently, forms 3 and 5 also were wide-spread, as each was secured from several widely separated localities. Form 6 was obtained from only 2 collections, 1 from Fergus Falls, Minn., in 1933, and the other from Owatonna, Minn., in 1934. Only two collections were obtained outside the flaxseed-producing area. One of these, collected at Astoria, Oreg., yielded form 7 and the other, gathered near Corvallis, Oreg., gave form 8. These two forms are very distinct from all those collected in the flaxseed area and also from each other. In 1934, forms 10, 11, and 13 were each obtained but once; form 9, twice; form 12, 4 times; and form 14, 9 times. Forms 12 and 14 were found in widely scattered localities in Minnesota and North Dakota. The latter form was obtained from more collections in 1934 than was any other.

Several forms have been obtained from the same locality, although the number of collections made in each has been rather limited. Forms 1, 2, 4, 12, and 14 have been obtained from 11 collections made near Fargo, N. Dak.; forms 1, 2, 3, and 4, from 5 collections made near Langdon, N. Dak.; forms 2, 4, 5, and 11, from 5 collections made at Cooncreek (near Anoka), Minn.; and forms 2 and 4, from 3 collections made at Mandan, N. Dak.

HOST RANGE AND VARIETAL RESISTANCE

The results of inoculating 165 varieties of flax with physiologic forms 1 to 5, inclusive, are given in table 3. As only 13 of the 165 varieties tested gave indications of being rust differentials, the reaction of each variety to each form has not been tabulated separately. The varieties have been grouped according to the flax type to which they belong. The percentages of plants of each variety that were immune, resistant, or susceptible are given, as is also the general rust reaction of each variety.

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction[1]
Linum usitatissimum crepitans (dehiscent flax):		*Percent*	*Percent*	*Percent*	
From Siberia	295	0	0	100	S
From Germany	496	0	0	100	S
From Ukraine	506	0	0	100	S
Do	507	0	0	100	S
L. usitatissimum (seed flax):					
Petals, broad, flat:					
Abyssinian:					
F. P. I.[2] 37086	36	0	0	100	S
F. P. I. 58762	300	0	0	100	S
F. P. I. 58764	302	3	9	88	S
From Egypt	380	12	9	79	S
From Fergana, S. E. Turkistan	511	0	56	44	D
F. P. I. 60559	701	48	10	42	D
From Kenya, East Africa	707	0	0	100	S

[1] Letters indicate the various types of rust reaction, as follows: D, differential variety (not reacting similarly to all forms); I, immune (75 percent or more of the plants immune); M, mixed (less than 75 percent of the plants falling into any 1 class); R, resistant (75 percent or more of the plants resistant); S, susceptible (75 percent or more of the plants susceptible).
[2] F. P. I. refers to accession number of the Division of Plant Exploration and Introduction.

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*—Continued

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction
L. usitatissimum (seed flax)—Continued.					
Petals, broad, flat—Continued.					
American:					
Blue-flowered:		*Percent*	*Percent*	*Percent*	
Bison	389	0	0	100	S
Blanc	323–c	0	0	100	S
Bolley No. 1823	754	9	0	91	S
Buda	270	0	54	46	D
Do	326	0	0	100	S
Diadem	321	2	31	67	D
Linota	244	0	0	100	S
Minnesota 24–410	421	0	0	100	S
Minnesota 25–202	447	0	0	100	S
Minnesota 25–221	423	0	0	100	S
Minnesota 25–245	446	0	0	100	S
Minnesota 281	438	0	0	100	S
North Dakota Resistant 5	411	0	0	100	S
North Dakota Resistant 52	275	0	0	100	S
North Dakota Resistant 114	489	0	0	100	S
North Dakota Resistant 714	399	0	0	100	S
North Dakota Resistant 726	412	0	3	97	S
North Dakota 40016	428	0	0	100	S
Pale blue	387–1	0	0	100	S
Redwing	320	0	0	100	S
Do	458	0	2	98	S
Do	499	0	51	49	D
Slope	274	0	0	100	S
Walsh	645	85	15	0	I
Winona	481	0	0	100	S
White-flowered:					
Ottawa white-flowered	24	0	0	100	S
Pink-flowered:					
Bolley Golden	644	70	30	0	M
Bolley No. 1821	751	100	0	0	I
Bolley No. 1822	750	100	0	0	I
Lethbridge Golden	23	5	5	90	S
Long No. 4	400	0	0	100	S
Long No. 66	337	0	0	100	S
Do	719	0	0	100	S
Long No. 83	354	0	0	100	S
Pale pink	173–1	0	100	0	R
Do	173–3	0	100	0	R
Do	649	0	100	0	R
Williston Golden	25	0	56	44	D
Argentine:					
North Dakota 1742	342	97	0	3	I
Minnesota 25–343	417	90	1	9	I
Minnesota 25–341	462	100	0	0	I
Minnesota 25–362	472	100	0	0	I
Minnesota 25–330	690	100	0	0	I
Minnesota 25–361–1	691	100	0	0	I
Minnesota 27–379–3	692	100	0	0	I
Minnesota 25–323	705	88	12	0	D
Biglow	414	97	0	3	I
Capa	720	21	53	26	M
Do	721	100	0	0	I
Do	722	94	6	0	I
Kenya	706	96	4	0	I
Do	709	80	18	2	D
Light mauve	379–1	24	76	0	R
Lino Grande	381–2	52	45	3	M
Long No. 5	466	94	6	0	I
Malabrigo	346	96	4	0	I
Do	696	100	0	0	I
Rio	280	100	0	0	I
Rosario	316	3	97	0	R
Indian:					
Howard and Khan (*13*):					
var. *luteum*, type 1	--------	0	0	100	S
var. *cyaneum*, type 8	--------	0	0	100	S
var. *purpureum*, type 11	--------	5	0	95	S
var. *albidum*, type 12	--------	34	0	66	M
var. *album*, type 15	--------	0	0	100	S
var. *agreste*, type 22	--------	0	0	100	S
var. *meridionale*, type 25	--------	0	0	100	S
var. *pratense*, type 28	--------	0	0	100	S
var *minor*, type 29	--------	100	0	0	I
var. *pulchrum*, type 34	--------	100	0	0	I
var. *commune*, type 46	--------	100	0	0	I
var. *commune*, type 48	--------	100	0	0	I

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*—Continued

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction
L. usitatissimum (seed flax)—Continued.					
Petals, broad, flat—Continued.					
Indian—Continued.					
Howard and Kahn (*13*)—Continued.		*Percent*	*Percent*	*Percent*	
var. *commune*, type 53	-------	99	0	1	I
var. *commune*, type 55	-------	0	99	1	R
var. *campestre*, type 68	-------	99	1	0	I
var. *sativum*, type 121	-------	41	59	0	M
Shaw, Khan, and Alam (*19*), type 124	710	29	71	0	M
Mediterranean:					
Beladi	377	75	25	0	I
Crete	31–1	57	28	15	M
Cyprus	689	55	4	41	M
Giza	378	100	0	0	I
Morocco	376–2	96	0	4	I
Russian:					
Akmolinsk	515	11	15	74	D
Do	520	17	3	80	D
Billings	184	2	2	96	S
Crimean	563	27	5	68	M
Damont	3	99	0	1	I
Fergana	512	0	0	100	S
Newland	188	96	3	1	I
North Caucasian	620	45	13	42	M
Novelty	140	0	19	81	S
Pale blue	176	5	95	0	R
Samarkand	514	5	16	79	D
Winter:					
Roman winter	470	40	8	52	M
Hybrid:					
Reserve × Morye	486	19	25	56	M
Saginaw × Ottawa 770 B	675	100	0	0	I
Do	676	100	0	0	I
Do	677	100	0	0	I
Winona × Ottawa 770 B	651	100	0	0	I
Do	652	100	0	0	I
Do	653	100	0	0	I
Do	654	92	0	8	I
Do	656	100	0	0	I
Do	657	100	0	0	I
Do	658	98	0	2	I
Do	660	3	0	97	S
Do	661	97	1	2	I
Do	662	100	0	0	I
Do	664	100	0	0	I
Do	667	100	0	0	I
Do	671	100	0	0	I
Do	672	100	0	0	I
Do	673	100	0	0	I
Do	674	100	0	0	I
Do	681	100	0	0	I
Do	682	100	0	0	I
Do	697	100	0	0	I
Do	711	2	34	64	M
Do	716	100	0	0	I
La Plata	324	91	5	4	I
Long No. 125	356	40	0	60	M
North Dakota 40046	492	93	4	3	I
Tammes light blue	332	100	0	0	I
Tammes pale blue	333	97	0	3	I
Petals, narrow, margins crimped:[3]					
Ecru-olive[4] seed	325	0	0	100	S
Minnesota 25–125	392	0	0	100	S
Minnesota 29–39	684	100	0	0	I
Minnesota 29–55	685	24	0	76	S
Minnesota 29–76	686	100	0	0	I
Minnesota 29–45	687	100	0	0	I
Ottawa 770 B	355	100	0	0	I
Ottawa 829 C	391	0	0	100	S
Pale blue	646	4	9	87	S
Tammes crimped	330	0	0	100	S
"Very pale blue crimped"	647	5	31	64	D

[3] The word "crimped" is here used to describe the petal margins, which are incurved and somewhat wavy.

[4] RIDGWAY, R. COLOR STANDARDS AND COLOR NOMENCLATURE. 43 pp., illus. Washington, D. C. 1912.

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*—Continued

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction
L. usitatissimum (fiber flax):					
Petals, narrow, margins crimped—Continued.					
Blue-flowered:		*Percent*	*Percent*	*Percent*	
Althausen	628	0	0	100	S
Do	630	7	0	93	S
Dalgonetz	498	0	0	100	S
F. I. No. 3	694	2	6	92	S
J. W. S.,[5] F. P. I. 73560	388	3	8	89	S
J. W. S	708	16	0	84	D
Peerless	695	1	0	99	S
Saginaw	449	7	3	90	S
White-flowered:					
Friesland white	56-1	0	0	100	S
Minnesota 25-64	420	0	0	100	S
Pinnacle	693	0	2	98	S
Saginaw white	448	0	0	100	S
Tammes white	329	0	0	100	S
Tammes yellow seed	331	0	0	100	S
Pink-flowered:					
Deep pink	648	0	0	100	S
Pale pink	479	0	0	100	S
Tall pink	451-3	0	1	99	S
Do	451-3	0	0	100	S
Tammes deep pink	334	0	0	100	S
Do	336	0	0	100	S

[5] J. W. S. are the initials of J. W. Stewart, the originator of the variety.

When 75 percent or more of the tested plants in a variety fell into a single reaction class, the variety, if not differential, was thought to possess the reaction of that class; when less than 75 percent of the tested plants fell into a single reaction class, the variety was considered as too heterogeneous to be classified and was termed "mixed." Approximately twelve 30-day-old plants of each variety were inoculated with each rust form, and in cases where the classification was in doubt the tests were repeated. The percentage figures, therefore, are based on the reaction of 60 or more plants.

The lack of genetic purity of the varieties for rust reaction was one of the striking features of this test. Thirty-nine varieties were pure for rust immunity, but twenty-two of these were Minnesota hybrids that had been selected particularly for this quality. Twenty-two additional varieties had from 75 to 99 percent of the plants immune. Twenty of these were classed as immune and two as differentials. In a majority of the varieties included in this group most of the plants lacking immunity were highly resistant. Fifty-three varieties were pure for susceptibility. An additional 22 had from 75 to 99 percent of their plants susceptible. Nineteen of these were classed as susceptible and three as differentials. Seven varieties were classed as resistant, 3 of which were pure for resistance and 3 showed plants either resistant or immune. Fourteen varieties were so heterogeneous that they could not be classified as to predominance of reaction, and were classed as mixed. Additional differentials might have been obtained from this last group, but their reactions to the five forms did not indicate them to be such. Thirteen varieties were found to contain rust-differentiating strains, and were classed as differential varieties.

The varieties and strains included in this test do not exhaust the possibilities for obtaining immune, resistant, or susceptible lines in any of the groups. These varieties were chosen because they were typical of the different groups and of diverse geographical origin or because they possessed commercial possibilities, and they probably are representative of their respective groups in regard to rust reaction. The dehiscent flaxes, *Linum usitatissimum* var. *crepitans*, were pure for rust susceptibility. This was the only major group in which all varieties and strains were consistently pure for one type of rust reaction. The American blue-flowered and white-flowered seed flaxes and the white-flowered and pink-flowered fiber flaxes were predominantly susceptible, but some varieties in both of these groups possessed plants that were either resistant or immune. The Abyssinian varieties and the blue-flowered fiber flaxes also were predominantly susceptible, but most of the varieties in these groups were mixtures in which some plants were either resistant or immune. The Saginaw × Ottawa 770 B hybrids were pure for immunity. The Winona × Ottawa 770 B hybrids and the Mediterranean and Argentine varieties were predominantly immune, but a number of varieties in these groups possessed plants the reactions of which ranged from complete immunity to extreme susceptibility. The other hybrids and the Russian varieties were heterogeneous in reaction, most varieties in these two groups having plants falling into all three rust-reaction categories. Varieties with petal margins crimped were relatively pure for rust reaction.

STABILITY OF PHYSIOLOGIC FORMS

Physiologic forms 1 to 4 of *Melampsora lini* have been in culture for approximately 4 years and have passed through 20 to 30 urediospore generations. In none of these forms nor in any of the others that have been studied has there been any indication of a change in pathogenicity.

DISCUSSION

The effect of the discovery of physiologic forms of *Melampsora lini* on measures to control this rust through the development and use of resistant varieties is, of course, problematical. Thus far, 14 physiologic forms have been distinguished by the reaction of seven differential hosts. It seems probable that more forms will be isolated when additional differentials are discovered and when more rust collections are studied. Allen (*1*) has shown that *M. lini* is heterothallic. The importance of this phenomenon in the origin of new forms of flax rust is not yet known. However, it has been demonstrated (*16*, *22*) that the aecial stage on the barberry is a fertile field for the development of new physiologic forms of *Puccinia graminis tritici* Eriks. and Henn. Since the process of aecial formation in the two rusts is comparable, there is no reason to believe that new forms of *M. lini* may not originate in the aecial stage on flax. The destruction of the common barberry, the aecial host of *P. graminis* Pers., would effectively prevent the production of new forms of *P. graminis* by hybridization. *M. lini*, however, is a eu-autoecious rust, and therefore to preclude the opportunity for the development of new rust forms through hybridization would necessitate the complete destruction of all rusted portions of flax plants from previous crops, an impracticable task.

Although *Melampsora lini* appears to be highly specialized, not only on various other species of *Linum* (*5, 8, 9, 17*), but, as has been demonstrated by the present tests, on *L. usitatissimum*, and although it possesses abundant opportunities for hybridization and the subsequent development of new forms, the prospects of rust control through the development of resistant varieties appear to be bright. The 165 varieties of flax showed surprisingly little specific response to five forms of flax rust. This is the more remarkable when it is considered that these 165 varieties represented the fruit of a systematic effort to obtain diverse types of *L. usitatissimum* from all parts of the world. Of the 165 varieties, 152 gave no indication of possessing rust-differentiating potentialities. Sixty-one varieties were predominantly immune from all five forms with which they were tested. Since these immune varieties comprised a number of flax types, and since Henry (*10*) has shown that immunity from flax rust is transferred independently of wilt resistance or morphologic type, there should be no lack of immune breeding material.

The breeding program, already in progress, for the development of rust-resistant varieties of flax, appears to rest on a sound basis. Henry (*10*) found Ottawa 770 B and certain strains of Williston Golden and Argentine to be immune from rust. In the present investigations, certain forms of rust were found to attack all strains of Williston Golden, but Ottawa 770 B and certain Argentine selections have been consistently immune. Henry used only the latter two as rust immune parents in his breeding work, and most of the Minnesota selections that have been derived from these crosses were immune from the five forms of rust with which they were tested. Thus far, there has been no evidence of the existence of a form of flax rust capable of attacking Ottawa 770 B, certain Argentine selections or varieties possessing similar factors for resistance. Nevertheless, it would be desirable to subject these immune varieties to rust collections from other parts of the world to determine whether forms capable of attacking them exist. Stakman, Levine, and Bailey (*21*) found White Tartar oats resistant to all forms of *Puccinia graminis avenae* Eriks. and Henn. collected in North America, but susceptible to forms of this rust obtained from Sweden and South Africa. If forms of *Melampsora lini* capable of attacking the immune flax varieties of the United States exist in other parts of the world, measures should be taken to assure their exclusion from this country, since it has been demonstrated that teliospores on bits of straw and chaff that are often present with the seed are carriers of flax rust (*10*).

The heterogeneous rust reaction of so many of the varieties was surprising. Apparently natural hybridization plays a more important role than has sometimes been supposed (*4*) or else the nursery technique is at fault. It appears more probable that the former is the case. Henry and Tu (*12*) found, under conditions at St. Paul, Minn., that natural crossing between varieties in adjacent rows or even in rows several feet apart was too important a factor to be neglected. Apparently, this condition prevails in other localities, since 70 of the 165 varieties studied gave heterogeneous rust reaction. Bagging of individual plants and isolation of the separate varieties in the field may be necessary in order to insure the maintenance of varietal purity. It is possible that a test to determine rust reaction, made in conjunction with the certification of rust-resistant varieties, would aid materially in maintaining varietal purity.

SUMMARY

Strains of Buda (C. I. 270), Williston Golden (C. I. 25), Williston Brown (C. I. 803), Akmolinsk (C. I. 515), J. W. S. (C. I. 708), Kenya (C. I. 709), "very pale blue crimped" (C. I. 647), Argentine (C. I. 705), and Abyssinian (C. I. 701) have been selected as differential varieties for the identification of physiologic forms of *Melampsora lini* (Pers.) Lév. on *Linum usitatissimum* L.

From 99 collections of *Melampsora lini* made in the United States and Canada, 14 physiologic forms have been distinguished by the reaction of the differential varieties named above.

Several forms of the rust were found to be widely distributed in Minnesota, North Dakota, South Dakota, Oregon, and Manitoba. In several localities more than one form was found.

In the 4-year period covered by these investigations four rust forms have passed through 20 to 30 urediospore generations without any apparent change in pathogenicity.

Pathogenicity tests indicated that as a rule flax varieties are not specific in their reaction to the different forms of rust. Of 165 varieties tested, only 13 gave differential reactions to five forms.

Pathogenicity tests showed that many varieties were not pure lines in respect to rust reaction. Lines pure for this characteristic have been readily obtained by a process of plant selection.

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