

THE GENETICS OF RUST REACTION TO SPECIFIC
COLLECTIONS OF RUST, MELAMPSORA LINI (PERS.) LEV.,
IN CERTAIN FLAX CROSSES

by

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ABSTRACT

Four varieties of flax (C.I. 1225, C.I. 1223, C.I. 1219 and C.I. 1218) were studied for reaction to three physiologic races of flax rust. Each of the four varieties was crossed with the tester varieties Bison, Dakota, Bombay and Crystal. Segregation of the resulting F₂ and F₃ populations was analyzed for reaction to each of the three races of rust (D-8, D-10 and 41). Results of the analysis were as follows:

1. A gene governing an immune reaction to all three races in C.I. 1225. This gene is allelic to the (L) gene assumed to be carried by Crystal.
2. Two genes governing an immune or resistant reaction to all three races in C.I. 1223. One of these genes is allelic to the (M) gene assumed to be carried by Dakota. The second gene is allelic to the (N) gene assumed to be carried by Bombay.
3. A gene governing an immune reaction to all three races in C.I. 1219. This gene was not allelic to any of the genes assumed to be carried by the tester parents.
4. Two genes governing an immune reaction to all three races in C.I. 1218. These two genes are different from the (M) and (N) genes assumed to be carried by Dakota and Bombay respectively. The relationship of these two genes to the gene or genes carried by Crystal is uncertain.

INTRODUCTION

Cultivated flax, Linum usitatissimum L., is the only one of about one hundred species of the genus Linum (47) that is cultivated. The chief useful products of the crop are the linseed oil, which is used in the paint and varnish industry, and the fiber which is used in the manufacture of linen. The flax rust fungus, Melampsora lini (Pers.) Lev., has been found to exist in all areas of the world where flax is cultivated, namely, North America, the Argentine, Russia, Europe, India, Australia and New Zealand. The disease, commonly known as 'flax rust', has occasionally been very destructive to the flax crop due to its occurrence in epidemic proportions. Several such epidemics have been reported in the United States between the years 1928 and 1951. In India the disease is responsible for an average annual reduction in yield of about 28% (34).

However, losses in yield due to rust have been reduced considerably in recent years, chiefly as a result of a systematic approach to the breeding of resistant varieties brought about by a knowledge of the physiologic races existing in a region and of the genes for resistance possessed by available host varieties.

The importance of the role that physiologic races have played in North America is illustrated in a number of varieties grown in the North Central States between the years

1931 and 1951. Bison, released as a wilt and rust resistant variety in 1926, has been susceptible to all collections of flax rust made in North America since 1931. Koto which was developed as a replacement for Bison, succumbed to rust while being increased for distribution in 1927. Dakota, Renew, Custer and Arrow were released as resistant varieties in 1946, but in 1948 races attacking these varieties were observed in North-western Minnesota and Eastern North Dakota. By 1952, the varieties B 5128, Marine, Redwood, Rocket and Sheyenne had replaced Dakota.

Melampsora lini (Pers.)Lev. differs from Puccinia graminis Eriks. and Henn., in that it is autoecious. The possible origin of new races through hybridization and genetic recombination, therefore, seems unlimited. That there are extensive recombinations in the sexual stage of M. lini was shown by Flor (13). He isolated 64 races from the F₂ progeny of a cross between race 22 from South America and race 24 from the United States. Of these, 62 were previously unknown, and some were more virulent on certain varieties of flax than either parental race.

In view of the complexity of the problem, it is imperative that new sources of resistance be explored and classified to provide for the eventuality of new races of flax rust found to be virulent on varieties now considered resistant. It is well known that varieties which are resistant in one region may be susceptible in another. It is also known

that South American races are widely virulent (18), attacking most of the varieties resistant in Australia, Europe and North America. It is therefore possible that introductions from South America could be valuable sources of resistance enabling plant breeders to deal more effectively with changes in the races prevalent in North America. This study was undertaken to determine the mode of inheritance of rust reaction in four flax varieties of Argentine origin.

LITERATURE REVIEW

I. The Host

1. Origin. Cultivated flax, Linum usitatissimum L. is an important commercial crop. According to Schilling (39) it originated through human selection from the wild species, L. angustifolium Huds., which is prevalent throughout the Mediterranean region and is the only species with which it can be crossed readily. Vavilov (42) maintained that cultivated flax was polyphyletic in origin.

2. Chromosome Number. Ray (35) reported haploid chromosome numbers of 8, 9, 10, 14 and 15 in 36 species of the genus Linum. There are conflicting reports as to the chromosome number in Linum usitatissimum. Several workers (6) report the haploid chromosome numbers of $n = 16$. However, many other workers report (5) the chromosome number of $n = 15$.

3. Sources of Rust Resistance. Varieties highly resistant in one region may be susceptible in another. Bison, universally susceptible to races in North America, Europe and South America, has been found to be immune in Australia (18). Bombay, which is susceptible to Australian races, was found to be immune to races prevalent in the Argentine (18). Twenty races isolated from European collections of flax rust resemble North American races in pathogenicity (18).

II. The Pathogen

1. History and Host Specialization. Persoon (32) described a rust fungus on L. catharticum and L. usitatissimum

in 1801. He named it Uredo minata B. lini. Leveille (28) transferred it to the genus Melampsora and called it Melampsora lini.

Arthur (2) demonstrated that Melampsora lini (Pers.) Lev. is eu-autoecious. While it is known that the rust of cultivated flax can perpetuate itself readily in the absence of any wild species of Linum, it is possible that some of them may serve to increase the inoculum. Arthur (2), Pethybridge et al. (33) and Miss Hart (22) obtained successful infection of L. lewisii, L. angustifolium and L. rigidum respectively with telial material from cultivated flax. Arthur (2) reports three additional species, L. breweri, L. congestum and L. Drymaroides, as hosts of Melampsora lini in California. Palm (31) from cross inoculation studies concluded that rust on cultivated flax was physiologically and, in some cases, morphologically distinct from that on certain wild flax species.

2. Life Cycle. Allen (1) demonstrated the heterothallic nature of flax rust. She stated that the immature teliospores are dicaryotic. During germination the nuclei fuse to produce the diploid phase. Two successive divisions of the diploid nucleus, one of which is a reduction division, result in 4 haploid nuclei which migrate into the 4 sporidia in the promycelium. Sporidial infection of a susceptible host results in the formation of a pycnium. Each pycnium is incapable of further development unless pycniospores from a

pycnium of opposite mating type are transferred to it. Then it develops into an aecium bearing dicaryotic aeciospores. The aeciospores reinfect flax, producing the dicaryotic uredial stage which repeats itself.

3. Physiologic Specialization. Physiologic races of rusts are dicaryotic clones identified by the types of infection produced on selected varieties termed 'host testers' or 'differentials' (18).

Henry (23) suspected the occurrence of physiologic forms of Melampsora lini (Pers.) Lev. on cultivated flax but did not demonstrate their existence. Physiologic specialization in M. lini was first demonstrated by Flor (8). He differentiated 14 races by the reaction of 9 flax varieties. Using additional differential varieties, Flor (9) identified 10 additional races.

Physiologic specialization of flax rust has also been demonstrated in Argentina by Vallega (41), in Europe by Straib (40), in Australia by Waterhouse and Watson (44) and Kerr (27), in India by Prasada (34) and in New Zealand by Cruickshank (4).

III. Epidemiology

The varieties of flax grown in North America between 1931 and 1951 largely determined the prevalence of the different races. Flor (17) indicated that since this rust attacks only species of Linum, the survival of a particular race depends upon the continued production of varieties susceptible to it. Races unable to attack the current commercial varieties

disappear, while those attacking the predominant varieties tend to increase. Bison was released as a rust resistant variety in 1926 (17) but it has been susceptible to all collections of flax rust made in North America since 1931 when physiologic race studies were started. Dakota, carrying the Newland gene for rust resistance, was released in 1946. In 1948, however, it was attacked in Minnesota and North Dakota (17). Koto was immune from rust during several years of nursery tests, but was attacked while being increased for distribution.

IV. Differential Varieties

1. Origin of Differentials. The flax varieties that differentiate physiologic races of Melampsora lini (Pers.) Lev., were selected by the trial and error method. Flor (9) tested the reactions of 50 varieties of flax to 36 rust collections made in 1931 and 1932. He found the reaction of individual plants of varieties possessing some resistance to be extremely variable. It was, therefore, necessary to develop lines from these varieties which were pure for rust reaction. This was done by individual plant selection. Following this procedure Flor (9) isolated 14 physiologic races by the use of 7 differentials. These were Williston Brown, Akmolinsk, J.W.S., Pale Blue Crimped, Kenya, Argentine selection (C.I. 705) and Abyssinian.

2. Isolation of Lines Bearing Unit Rust Conditioning Genes. Differential lines possessing single rust-conditioning

genes usually show less variation in infection type than do lines with 2 or more genes. Flor (18) stated that if each host tester possessed a single gene for rust resistance, race determinations would give a more nearly complete indication of pathogenicity, and the identification of rust resistant genes in varieties would be simplified.

Flor (18) in 1954 revised the flax rust differential varieties. Although two of the old differentials were dropped because they gave little information or had unsatisfactory reactions there was little loss in continuity of race identification as 16 of the 18 new differentials either were old differentials or were derived from those previously used. He developed these lines pure for each rust conditioning gene by backcrossing to Bison.

V. Inheritance of Pathogenicity

Flor (13) studied the reactions of sixteen rust differentiating varieties to races 6, 22 and 24, and to selfed cultures of these races. He also studied the F₁ and F₂ hybrid cultures of race 22 crossed with race 24 and race 6 crossed with race 22. He found that virulence was inherited as a recessive character, since F₁ cultures were unable to attack varieties resistant to either parent race. Varieties susceptible to both parent races were susceptible to the F₁ culture. Out of 133 F₂ cultures segregation ratios of 1:3, 1:15 and 1:63 of virulence : avirulence were obtained. The only exception was from the variety Williston Brown. In this instance a