

Genetics of Rust Resistance of Six Argentinian Flax Introductions

D. E. Zimmer and G. D. Statler

Research Plant Pathologist, Agricultural Research Service, U.S. Department of Agriculture, and Associate Professor, Department of Plant Pathology, North Dakota State University, Fargo, North Dakota 58102.

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ABSTRACT

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Six Argentinian introductions of seed flax (*Linum usitatissimum*) resistant to races of *Melampsora lini* that collectively attack lines monogenic for known genes for resistance except M^6 and P^4 , were analyzed genetically for previously unknown rust-resistance genes. The F_2 segregation ratios for resistance to races 1, 22, 73, and 312, between each introduction and Bison, was explained without postulating the existence of any unknown genes. All

introductions were postulated to contain the N gene. Cereal introductions C.I. 2834 and C.I. 2837 also possessed a gene that conditioned resistance against races 1, 73, and 312, but was ineffective against race 22. Cereal introductions C.I. 2829, C.I. 2830, C.I. 2834, and C.I. 2835 possessed two additional genes that were differentially effective against two or more of the tester races.

Rust incited by *Melampsora lini* (Ehrenb.) Lev. can be a serious disease of seedflax, *Linum usitatissimum* L., in Canada and the United States (1). During the past 50 years, severe losses generally have been avoided by growing resistant cultivars. Step-wise changes in the virulence of the native rust population during this time have necessitated repeated replacement of established cultivars with those resistant to the new races (4, 6). Replacement cultivars like Bison (released in 1927), Koto (1943), Dakota (1946), Sheyenne (1947), Redwood (1951), Marine (1952), Arny (1961), Cree (1962), Summitt (1963), Bolley (1964), Linott (1966), Nored (1968), and Culbert (1975) generally have contained single additional genes for resistance and have enhanced further step-wise changes in virulence. If this procedure continues and new sources of resistance are not discovered to replenish the germplasm pool, the reservoir of genes conditioning resistance to the North American flax-rust population will be depleted.

The virulences of *M. lini* races vary among the major flax-producing areas of the world (3). Until the discovery of the M^6 and P^4 genes in introductions from Pakistan and Hungary, none of the other 26 genes was known to condition resistance to the native Argentinian flax-rust population (3, 5). Flax breeding lines free of rust in Argentina would be likely sources of new rust-resistance genes for use in North American flax breeding programs. This study was undertaken to elucidate genetically the rust resistance of six Argentinian flax introductions, in hope of discovering previously unknown rust-resistance genes.

MATERIALS AND METHODS

Seed of six Argentinian flax selections were obtained from Agriculture Canada, Morden, Manitoba, and

assigned Cereal Introduction (C.I.) numbers 2829, 2830, 2833, 2834, 2835, and 2837. Preliminary tests with a composite of races that caused rust in all flax except those conditioned by genes L^6 , M^3 , N^1 , P^2 , P^3 , and P^4 suggested these lines as probable sources of new genes for rust resistance (*personal communication*, J. A. Hoes, Agriculture Canada).

Because races are unavailable to differentiate the M^6 and P^4 genes or identify many combinations of the remaining 26 resistance genes, we cannot establish the presence of genes solely by selective pathogenicity from available rust races. A genetic analysis of F_2 progenies between the new line and tester lines is required to unequivocally establish the existence of new rust-conditioning genes.

Crosses were made between Bison (C.I. 389), a cultivar susceptible to known North American races, and each introduction. Thirty 4-week-old seedlings of each introduction, 20 F_1 plants of each cross, and 67 to 1,159 F_2 progenies from randomly selected F_1 plants were inoculated separately with races 1, 22, 73, and 312. These races differ widely in pathogenicity and collectively attack cultivars that contain all known rust-resistance conditioning genes except M^6 and P^4 .

Plants were dusted with a 1:20 mixture of urediospores and talc. After inoculation the plants were lightly misted with water, placed overnight in a humidity cabinet at 18 C, returned to greenhouse benches, and maintained at 20 \pm 2 C. Rust readings were taken 10 days later.

RESULTS AND DISCUSSION

Each of the introductions and F_1 's of crosses with Bison showed uniform and complete resistance to races 1, 22, 73, and 312, indicating that unknown genes might be involved. The segregation ratios obtained in the F_2

TABLE 1. Chi-square tests for goodness fit to hypothetical genetic ratios in F₂ progenies of crosses between the rust-susceptible cultivar Bison and six Argentinian flax introductions with undetermined genes for resistance.

Cross	Race	Observed ratio		Goodness of fit		
		Resistant	Susceptible	Ratio	χ^2	<i>P</i> value
Bison × C.I. 2829	1	1146	13	63:1	1.46	> 0.10
	22	947	308	3:1	0.33	> 0.50
	73	80	24	3:1	0.20	> 0.50
	312	247	69	3:1	2.56	> 0.10
Bison × C.I. 2830	1	875	13	63:1	0.06	> 0.80
	22	875	43	15:1	3.84	> 0.05
	73	135	43	3:1	0.36	> 0.80
	312	257	19	15:1	0.19	> 0.50
Bison × C.I. 2833	1	148	11	15:1	0.12	> 0.50
	22	116	39	3:1	0.00	> 0.95
	73	92	24	3:1	1.15	> 0.25
	312	241	89	3:1	0.68	> 0.25
Bison × C.I. 2834	1	486	8	63:1	0.01	> 0.90
	22	409	85	3:1	16.00	< 0.01
	73	52	15	3:1	0.24	> 0.50
	312	170	55	3:1	0.03	> 0.80
Bison × C.I. 2835	1	768	11	63:1	0.12	> 0.60
	22	731	38	15:1	2.26	> 0.10
	73	193	62	3:1	0.06	> 0.80
	312	314	27	15:1	1.56	> 0.20
Bison × C.I. 2837	1	813	58	15:1	0.25	> 0.50
	22	640	231	3:1	1.07	> 0.25
	73	297	96	3:1	0.07	> 0.75
	312	249	87	3:1	0.17	> 0.60

generations, however, failed to substantiate this. Had a single gene for resistance been operative, the F₂ progenies would have segregated in monogenic ratio to tester races. We obtained monohybrid, dihybrid, and, in some cases, trihybrid segregation ratios of all F₂ progenies tested with races 1, 22, 73, and 312 (Table 1).

Resistance to race 1.—Segregation for resistance to race 1 within F₂ progenies of Bison with C.I. 2829, C.I. 2830, C.I. 2834, and C.I. 2835 fit a trihybrid ratio ($P > 0.10$, 0.80, 0.90, and 0.60, respectively). Segregation within F₂ progenies of Bison with C.I. 2833 and C.I. 2837 fit a dihybrid ratio ($P > 0.50$ and 0.50, respectively). Race 1 is virulent only on varieties whose resistance is conditioned by L^1 , L^9 , M^1 , and M^2 of the 28 known genes. Consequently, many combinations of genes could result in the observed dihybrid and trihybrid ratios.

Resistance to race 312.—Segregation for resistance to race 312 in F₂ progenies of Bison with C.I. 2829, C.I. 2833, C.I. 2834, and C.I. 2837 fit a monohybrid ratio ($P > 0.10$, 0.25, 0.80, and 0.60, respectively). Segregation in F₂ progenies of Bison with C.I. 2830 and C.I. 2835 fit a dihybrid ratio ($P > 0.50$ and 0.20, respectively). In all cases, fewer genes conditioned resistance to race 312 than to race 1. Race 312 is virulent on lines with resistance conditioned by L^1 , L^9 , M^1 , and M^2 genes (as with race 1) and K , L , L^2 , M , and M^4 genes. It is therefore possible that the new introductions contained either the K , L , L^2 , M , or M^4 genes.

Resistance to race 73.—The segregation for resistance

to race 73 within F₂ progenies of Bison and the introductions satisfactorily fit a monohybrid ratio ($P > 0.25$). Race 73 is virulent on cultivars whose resistance is conditioned by L , L^1 , L^9 , M , M^1 , and M^2 (genes ineffective against race 1 and race 312) and N , M^3 , P , L^5 , and L^7 genes. Race 73, unlike race 312, is avirulent on cultivars with resistance from K , L^2 , or M^4 genes. Four known genes, L^5 , L^7 , M^3 , and P , were effective against races 1 and 312 and ineffective against race 73. Thus, the monohybrid ratio for resistance to race 73 could be explained by assuming that each of the introductions contains either the K , L^2 , or M^4 genes.

Resistance to race 22.—Segregation for resistance to race 22 within F₂ progenies of Bison with C.I. 2830 and C.I. 2835 fit a dihybrid ratio ($P > 0.05$, and 0.10, respectively), whereas segregation within F₂ progenies of Bison with C.I. 2829, C.I. 2833, and C.I. 2837 fit a monohybrid ratio ($P > 0.50$, 0.95, and 0.25, respectively). The segregation within F₂ progenies of Bison with C.I. 2834 did not fit a 3:1 ratio. The observed ratio of 409 resistant to 85 susceptible, however, more nearly fit a monohybrid ratio than a dihybrid ratio. The deficiency of the susceptible class may have been a result of gametic selection, abnormal disjunction, or zygotic or gametic lethality.

Race 22 is virulent on lines with resistance conditioned by all known genes except L^2 , M^6 , N and P^4 . Any of these genes singularly could account for the monohybrid ratio to race 22 and any two of them for the

dihybrid ratio. It was unlikely that the resistance to race 22 exhibited by the six Argentinian introductions was a result of either the M^6 or P^d genes, as these genes were only recently identified in introductions from Hungary and Pakistan (5). However, the L^2 and N genes have been known for over 30 years and have been widely distributed around the world. Flor (2) reported that the N gene conditioned resistance against the South American races; thus, its use in breeding programs and its presence in introductions from South America would not be surprising.

The monohybrid and dihybrid ratios for resistance to race 22 can be reconciled to the monohybrid, dihybrid, or trihybrid ratios for resistance to races 1, 312, and 73, without postulating the existence of new genes for rust resistance. Under such a system, C.I. 2829 and C.I. 2834 would possess the N genes, effective against races 1, 22, and 312, and two other genes: one that conditions resistance against race 1, and one that conditions resistance to races 1 and 73 and is ineffective against races 22 and 312. Two genes (L and M) are known to condition resistance to race 1 and to be ineffective against races 22, 73, and 312. Two genes (K and M^4) condition resistance to races 1 and 73 and are ineffective against races 22 and 312. Thus, C.I. 2833 and C.I. 2837 would possess the N gene and either gene (K or M^4) effective against race 1 and 73 and ineffective against races 22 and 312. Cereal introductions C.I. 2830 and C.I. 2835 would possess the N gene; the L^2 gene, effective against races 1, 22, and 73; and another known gene (L^5 , L^7 , M^3 , or P), effective against races 1 and 312 and ineffective against races 22 and 73.

The rust-resistance genotype of the new introductions can be unequivocally established only through genetic analysis of F_2 progenies of crosses between known monogenic rust-resistant lines and each introduction. Such effort appears to be unwarranted, as any gene discovered would probably not condition resistance

against all known races and would be of limited value in a breeding program.

The failure to identify positively unknown rust-resistance genes with broad race coverage in six introductions illustrates the difficulties to be encountered in future years as the search for new resistance genes continues among flax introductions. The 28 rust-resistance genes identified in the United States have been distributed around the world and have been used in numerous breeding programs. Such efforts will continue to result in the development of a combination of known genes that produce the same response to known tester races as would be expected from an introduction containing a single unknown rust-conditioning gene. Until a complete set of tester races is developed that identifies each of the known genes for resistance, genetic tests will be required to establish whether combinations of known genes are involved.

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