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Recombination among genes at the *L* group in flax conferring resistance to rust

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Summary. Fourteen of the known genes conferring resistance to rust in flax occur in the *L* group, and recombinational analysis has been used to study their fine structure. Three important features were observed. (a) Similar to the findings of Shepherd and Mayo, only susceptible recombinants were detected among the testcross progeny of 11 of the 15 heterozygotes involving pairs of *L* genes. Some of these recombinants showed variation in the degree of their susceptibility and appeared to be unstable in nature. (b) A new class of recombinants exhibiting a modified type of resistance was recovered. They occurred rarely but consistently, with frequencies similar to that of susceptible recombinants. (c) Rare resistant plants occurred among the progeny of susceptible recombinants. In each case, the specificity of the resistant plant corresponded to only one of the parental types. The relative roles of seed contamination, mutation, recombination and the transposition of genetic elements are discussed to account for these features.

Key words: *Linum* spp. – *Melampsora lini* – Fine structure – Recombination – Reversion

Introduction

Genes conferring resistance to plant diseases frequently occur grouped together in the host chromosomes. Such grouping has been shown in numerous well-documented plant disease systems of agricultural importance including the flax – flax rust, wheat – stem rust, maize – maize rust and barley – powdery mildew systems (for recent references, see Jones 1988; McIntosh et al. 1988; Hooker 1985; Jahoor and Fischbeck 1987). However, it has been difficult to determine whether the genes within these groups are closely-linked or allelic, and these two gene arrangements have quite different theoretical and practical implications (Shepherd and Mayo 1972).

Early attempts to distinguish allelism and close linkage between genes conferring rust resistance in flax involved searching for recombinants among F_2 (Flor 1947; Kerr 1960), F_3 (Myers 1937; Flor 1941) or testcross progeny (Kerr 1960) of plants heterozygous for the two genes. None of these identified recombinants unequivocally. This is not surprising, since relatively small numbers of progeny were raised from heterozygotes with the genes present in the repulsion phase. Later, Shepherd and Mayo (1972) pointed out that recombination alone is not sufficient evidence to distinguish between close linkage and allelism. To establish allelism, it is necessary to show that such genes control the same function. The *cis-trans* test has been widely used to determine the functional identity of genes; but this test is not directly applicable to certain groups, including genes conferring resistance to plant diseases, whose expression are co-dominant. Instead, Shepherd and Mayo (1972) proposed a 'modified *cis-trans*' test where the *cis* phenotype could provide the diagnostic information required.

Thus, using large numbers of progeny, the analysis of genes conferring resistance to plant diseases has been further developed. Tests on the 'fine structure' of genes within a group have been carried out in three host-parasite systems; namely, genes in maize (Saxena and Hooker 1968, 1974; Bergquist 1981) and flax (Shepherd 1963; Flor 1965; Shepherd and Mayo 1972; Mayo and Shepherd 1980) conferring resistance to their rusts, and in barley conferring resistance to powdery mildew (Jørgensen and Moseman 1972; Giese et al. 1981; Wise and Ellingboe 1985).

In *Linum* spp., known genes conferring resistance to rust occur in six groups, namely, *K, L, M, N, P* and *D*

Table 1. Reaction of differential cultivars possessing different *L* genes to the rust strains employed in this study

Differential cultivar	C.I.[a] no.	Gene[b]	Host reaction[c] to individual rust strains								
			A	B	C	D	E	F	G	H	I
Ottawa 770B	355	*L+P5*[d]	0	0	0	0	0	4	0	0	0
B^{14} × Burke	B^{14}–1180	*L1*	4	2–3	1	0	3	3	4	4	4
Stewart	1072	*L2*	4	0	0	0	0	0	0	4	4
Pale Blue Crimped	647	*L3*	0	0	1	0	4	1	0	1	0
Kenya	709	*L4*	0	0	0	0	3	0	0	0	0
Wilden	1193	*L5*	0	0	0	4	0	0	0	2	3
Birio	1085	*L6*	0	0	0	4	0	0	0	0	3
Barnes	1190	*L7*	0	0	2	4	0	1	4	4	4
Towner[e]	–	*L8*	0	4	4	0	4	1	4	4	4
Bison	389	*L9*	0	4	4	4	4	4	4	0	0
Bolley Golden Seln.	1183	*L10+R*[f]	0	0	1	0	2–3	1	4	0	4
B^f × B.G.S.	B^f–1183	*L10*	0	0	1–2	0	4	1	4	3	4
L11	[g]	*L11*	0	0	4	0	0	0	0	0	0
Lx	[h]	*Lx*	0	0	0	4	0	0	4	2	4
Hoshangabad	[i]	none	4	4	4	4	4	4	4	4	4

[a] C.I. = Cereal Introduction number, United States Dept. of Agriculture
[b] Flor (1956), Kerr (1960) Flor and Comstock (1972) and Mayo and Shepherd (1980)
[c] Reactions: 0–immune, 1–resistant, 2–intermediate, 3–moderately susceptible and 4–susceptible
[d] Cultivar Ottawa 770B carries a second gene, *P5*, recognized by rust strain A (Kerr 1960)
[e] Stock of Towner carrying host gene *L8* obtained from D.A. Jones, Dept. of Genetics, University of Adelaide. Initial stock used did not carry this gene (Jones 1988)
[f] Cultivar Bolley Golden Seln. carries a second gene *'R'* not yet isolated as a differential (K.W. Shepherd, personal communication)
[g] C.I. number not known
[h] Experimental line derived by rare recombination within *L6* (Mayo and Shepherd 1980)
[i] Obtained from Waite Agricultural Research Institute, accession number W.I. 89

(Misra 1966; Jones 1988). A critical difference was observed in the recombinational behaviour of genes from the *M* group as against those from the *L* group. In the *M* group, both susceptible and resistant recombinants were detected (Flor 1965; Mayo and Shepherd 1980). Furthermore, among the progeny of resistant recombinants with *MM3* in coupling, rare resistant plants having the separate *M* and *M3* parental specificities were recovered (Mayo and Shepherd 1980). This observation confirmed the reciprocal nature of recombination between these genes and supported the conclusions that genes from the *M* group are situated at separate closely-linked loci and function independently of each other.

In the *L* group, among testcross progeny of plants heterozygous for *L2L10* in repulsion phase, Shepherd and Mayo (1972) detected only susceptible recombinants. Since no resistant recombinants were recovered, it was suggested that perhaps resistant recombinants were produced, but *L2* and *L10* interact together on the same linear strand, in *cis*, preventing the resistant recombinant genotypes being expressed phenotypically. They argued that both *L2* and *L10* specificities should be recovered among progeny of approximately half of the susceptible recombinants. When this hypothesis was tested, they recovered rare revertants expressing only *L10*, and not *L2*, specificity.

Shepherd and Mayo (1972) also detected four susceptible recombinants among testcross progeny of the *L2L6* heterozygote, using a rust strain avirulent on both *L2* and *L6* parental specificities. Later, the progeny of all four susceptible plants were tested with a different rust strain, also capable of recognizing both *L2* and *L6*. Surprisingly, whilst one family produced only susceptible progeny, the other three families segregated in a ratio of 3 resistant to 1 susceptible, indicating the presence of a new specificity, provisionally named *Lx* (Mayo and Shepherd 1980).

The apparently complex nature of genes belonging to the *L* group called for further investigation, and recombination between other genes from this group are reported here.

Materials and methods

The host cultivars used, together with their reactions to an array of rust strains, are listed (Table 1). The cultivar Hoshangabad does not carry any known genes conferring resistance to flax rust.

Two types of crosses were made: (a) Testcrosses. F_1 plants, heterozygous for two different *L* genes, were used as females in crosses with Hoshangabad or Bison as the susceptible male parent. (b) Double crosses. Two F_1 plants, each heterozygous for

two different *L* genes, were crossed together, similar to the procedure used by Knott (1982) to study stem rust resistance in wheat. The advantage of this approach is that by choosing two appropriate strains of rust (avirulent on both genes present in one F_1 but virulent on both genes in the other F_1) and with sequential testing, susceptible recombinants from both of the heterozygotes involved can be detected in the same progeny population.

The techniques of rust inoculation and scoring types of rust infections are similar to those described by Flor (1954). The procedure used to screen testcross progeny for recombinants followed that of Shepherd and Mayo (1972). Progeny were first screened with a rust strain avirulent on both parental specificities, and those progeny showing a qualitatively greater degree of pustule development than the parental types were selected as putative susceptible recombinants. When the appropriate rust strains were available, the remaining testcross progeny were sequentially inoculated with two more rust strains, specific for each parental gene, to screen for resistant recombinants having both parental specificities.

The putative susceptible recombinants were raised in strict isolation during flowering from all other flax plants, to prevent pollen contamination. Care was also taken to avoid contamination of seed from other plants at harvest. The progeny of putative susceptible recombinants were rust-tested to confirm their phenotype and to search for rare resistant revertants.

Results

Testcrosses

Of 11 testcrosses analysed, 9 produced one or more susceptible recombinants among their progeny (Table 2). However, no confirmed resistant recombinants were recovered among testcross progeny from any of the heterozygotes.

Non-parental phenotypes

Resistant recombinants. With heterozygote *L7L10,* 17 plants appeared to show resistance to all three tester rust strains and they were kept for further testing. However, none of the plants showed definite immune flecks. Progeny tests of all 17 plants using rust strains specific for *L10* and then for *L7* demonstrated that each family possessed only one gene conferring resistance and, hence, they were reclassified as parental types.

Susceptible recombinants. In contrast, putative susceptible recombinants were detected among testcross progeny of the *LL7, LL11, L2L11, LL10, L7L10, L10Lx, LL6, LLx* and *L3Lx* heterozygotes (Table 2). The phenotype of these susceptible recombinants varied. Those detected among testcross progeny of *LL7, LL11, LL10, L10Lx* and *LL6* gave only type 4 reactions, whereas recombinants from other heterozygotes had intermediate reaction types of 3, 2–3 and even 2 (Table 3). For example, three recombinants from the *L3Lx* heterozygote gave reactions of type 2–3, 3 and 4. Again, certain recombinants from the *L2L11* heterozygote appeared to be unstable, giving an initial reaction of type 2 or 3, which changed to type 4 a few days later.

Table 2. Recombination between genes for resistance at the *L* group in flax

Genotype of F_1 heterozygote	No. of testcross progeny examined	Plants with parental phenotypes	Plants with non-parental phenotypes		
			Resistant recombinant	Susceptible recombinant	Modified resistant
Test crosses					
LL5	4,477	4,477	0	0	0
L2Lx	3,624	3,624	0	0	0
LL7	3,519	3,517	–	2	0
LL11	3,933	3,931	–	2	0
L2L11	4,676	4,671	–	5	0
LL10	13,078	13,073	–	5	0
L7L10	4,356	4,348	0	8	0
L10Lx	4,043	4,038	0	4	1
LL6	1,676	1,672	0	2	2
LLx	7,578	7,570	0	4	4
L3Lx	5,062	5,053	0	3	6
Double crosses					
LL9	4,098	4,098	–	0	0
L5Lx	4,098	4,098	–	0	0
L2L10	3,524	3,517	–	7	0
L6L9	3,524	3,523	–	1	0

– = not detectable with the method of analysis used

With the heterozygote *LLx,* testcross progeny of one batch were initially screened with a rust strain, A, that recognizes *L* and *Lx,* and three susceptible recombinants were detected. Surprisingly, two additional susceptible recombinants were detected when these same progeny were screened with the second and third rust strains, which recognize *L* and *Lx,* respectively. The failure to detect these recombinants with the first rust strain was ascribed to the likely presence of gene *P5,* since Kerr (1960) showed earlier that cultivar Ottawa 770B carries *P5* in addition to gene *L,* and we found that rust strain A recognizes gene *P5.* To test this hypothesis, rust strain B, which recognizes *L* and *Lx* but not *P5,* was used to progeny test these recombinants. Unexpectedly, the progeny of both recombinants segregated in a ratio of 3 resistant to 1 susceptible, contradicting the earlier conclusion that they possessed *P5.* Instead, these plants appear to express a modified type of resistance, as described below.

Recombinants with modified resistance. More plants with a modified type of resistance were detected among additional testcross progeny of the *LLx* heterozygote and of heterozygotes *L10Lx, LL6* and *L3Lx* (Table 2). These

Table 3. Rust reaction of susceptible recombinants and their progeny, including revertants

F_1 Het.	Plant no.	Sus. recombinant		Progeny				
		Rust[a] strain	Reaction[b]	Rust[a] strain	Reaction[b]	Total no. tested	No. of revertant	Specificity
LL7	(i)	B	4	B	4	1318	1	*L7*
	(ii)	B	4	B	4	528	0	
LL11	(i)	B	3–4	B	3–4	150	0	
	(ii)	B	4	B	3–4	139	0	
L2LL11	(i)	B	3[c] → 4[d]	B	1 ↔ 3[f]	104	–	
	(ii)	B	2 → 4	B	0 ↔ 2	44	–	
	(iii)	B	2 → 4	B	0 ↔ 2	120	–	
	(iv)	B	3/1[e]	B	1 ↔ 3	79	–	
	(v)	B	4/1–2	B	1 ↔ 3	102	–	
LL10	(i)	A	4	B	4	5633	0	
	(ii)	B	4	B	4	3488	0	
L7L10	(i)	B	4	B	4	1097	0	
	(ii)	B	2	B	2	2346	0	
	(iii)	B	4	B	4	1839	0	
	(iv)	B	2	B	2	3616	0	
	(v)	B	4	B	4	998	0	
	(vi)	B	4	B	1 ↔ 4	1745	–	
L10Lx	(i)	B	4	B	4	1788	0	
	(ii)	B	4	B	4	863	0	
	(iii)	B	4	B	4	200	0	
	(iv)	B	4	B	4	154	0	
LL6	(i)	B	4	B	4	114	0	
	(ii)	B	4	B	4	17	0	
LLx	(i)	A	3	B	4	801	0	
	(ii)	A	2–3	B	4	934	0	
	(iii)	A	2	B	3–4	1428	2	Both *Lx*
	(iv)	B	4	B	4	1644	1	Unresolved
L3Lx	(i)	B	4	B	2 ↔ 4	57	–	
	(ii)	B	3	B	4	50	0	
	(iii)	B	2–3	B	3–4	56	0	
L2L10	(i)	D	3	D	4	311	0	
	(ii)	D	3	D	4	543	0	
	(iii)	D	2–3	D	4	130	0	
	(iv)	D	3	D	4	352	0	
	(v)	D	3	D	4	1028	2	Both *L10*
	(vi)	D	2	D	3–4	451	0	
	(vii)	D	3	D	4	1814	0	
L6L9	(i)	H	3	H	4	1935	0	

[a] Refer to Table 1
[b] Reactions: 0–immune, 1–resistant, 2–intermediate, 3–moderately susceptible and 4–susceptible
[c] Initial score
[d] Later score
[e] Score of top/bottom leaves
[f] Continuous range of reactions
– Not detectable

plants are phenotypically distinct in a population and infected leaves show a characteristic marked spreading type of necrosis (reaction type 0n), usually with no pustules, but occasionally pinhead-sized pustules develop in the necrotic regions.

Revertant phenotypes

Progeny of putative susceptible recombinants were routinely rust-tested to confirm the phenotype of the original recombinants as well as to search for possible rare resistant revertants. Usually, the reaction type of the susceptible recombinants was repeated in the progeny, that is, plants with type 4 reaction had progeny showing type 4 reactions and plants with type 2 reaction had progeny giving type 2 reactions (Table 3). However, in a few cases, the reaction types of parents and progeny varied. For example, with the *L2L10* heterozygote, recombinant plant (iii) with type 2–3 reaction gave all type 4 progeny

whereas with *L7L10*, recombinant (iv) with a type 4 reaction gave progeny showing a continuous range of reaction varying from type 1 to 4 (Table 3). However, rare resistant revertants were detected among the progeny of susceptible recombinants from heterozygotes *LL7* (1 in 1,318) and *LLx* (2 in 1,428). The revertant from the *LL7* heterozygote was shown to possess *L7* specificity and the two from *LLx* had *Lx* specificity, with one expressing the modified type of resistance.

Double crosses

The four heterozygotes were tested in two sets of double crosses, namely *LL9* and *L5Lx* in the first combination and *L2L10* and *L6L9* in the second (Table 2). In the double cross analyses, at least four rust strains with appropriate specificity were required to detect resistant recombinants and, hence, no attempt was made to search for such plants.

Non-parental phenotypes

Susceptible recombinants. No susceptible recombinants were detected when the progeny of heterozygotes *LL9* and *L5Lx* were sequentially tested with the appropriate two strains of rust. However, eight susceptible recombinants were detected among the progeny of heterozygotes *L2L10* and *L6L9* with seven coming from the *L2L10* heterozygote and one from *L6L9* (Table 2). All of these recombinants showed type 2–3 reactions (Table 3).

Revertant phenotypes

No resistant revertants were detected among the progeny of the *L6L9* susceptible recombinant, but two revertants with *L10* specificity were detected among progeny of one of the seven susceptible recombinants of the *L2L10* heterozygote (Table 3).

Discussion

Shepherd and Mayo (1972) drew attention to two unusual features in their recombinational analysis of *L2* and *L10* genes: (i) Only one of the two expected classes of reciprocal crossing over (susceptible recombinants) was detected among testcross progeny. (ii) Some of the susceptible recombinants produced rare resistant plants among their progeny, but they all had the same specificity (*L10*).

We have now examined a much wider range of *L* gene combinations in recombinational studies and, again, rare susceptible plants were detected in most cases (Table 2). Because these plants occurred with a very low frequency, before accepting them as true recombinants we need to exclude the possibility that they might have arisen from seed contamination or mutation of one of the *L* genes in the F_1 hybrid. The morphology and flower colour of progeny of the susceptible plants were used to rule out seed contamination, but because of the lack of closely linked marker genes it was not possible to rule out mutation. In experiments designed to screen for spontaneous mutation of genes at the *L* group in flax, no confirmed mutants were observed among a total of 63,190 gametes coming from four different experiments involving eight different *L* genes, with a range of 4,478–9,701 gametes for each gene (Islam et al., in preparation). These data suggest then that most, it not all, of the susceptible plants detected in the present study had a recombinational rather than a mutational origin, and hereinafter they will be referred to as recombinants. However, some doubts must remain about their true origin since rare spontaneous mutation to susceptibility has been observed at the *Rp1* locus of maize (Saxena and Hooker 1968; Pryor 1986; Bennetzen et al. 1988) and the *ml-o* locus in barley (Jørgensen and Jensen 1979).

Although most of the susceptible progeny detected had type 4 reaction, some showed intermediate reaction (types 3, 2–3 and even 2). The progeny of recombinants usually showed the same degree of susceptibility as the original plant, but there were some exceptions where the progeny showed either more or less susceptibility than the original recombinant. Such phenotypic differences between parents and progeny could result simply from the different temperatures prevailing at the time of testing, since the tests were not conducted in strictly controlled environments and it is well known that temperature can affect the phenotype of certain gene-for-gene interactions between flax and its rust (Statler 1979; Islam et al., in preparation). On the other hand, this variation in susceptibility might have a genetic basis, since Bennetzen et al. (1988) reported that susceptible plants resulting from *Mutator*-induced changes at the *Rp1* locus in maize segregated for intermediate levels of resistance in their progeny. Currently we are attempting to distinguish between these two possible explanations.

When progeny of the susceptible recombinants were screened for revertants, rare resistant plants were only recovered among the progeny of three heterozygotes, namely, *LL7*, *LLx* and *L2L10* (Table 3), and in each case they had only one of the parental specificities, viz., *L7*, *Lx* and *L10*, respectively, although the number of revertants recovered was not large enough to exclude the possibility that the abscence of one parental specificity was due to chance. Thus, these results are similar to the earlier findings of Shepherd and Mayo (1972) with the *L2L10* susceptible recombinants.

In addition to the susceptible recombinants recovered, a feature of our results was the occurrence in some testcross populations of plants expressing a modified form of resistance (type 0n) different to that of either parent gene. Since these plants occurred with a similar

frequency to that of the susceptible recombinants, it was thought they may represent the *cis* products of recombination as postulated earlier by Shepherd and Mayo (1972). This hypothesis has not yet been critically tested by searching for both parental *L* gene specificities among the progeny of plants with modified resistance. However, some recent observations indicate that some of these plants may carry a completely different specificity for rust resistance to that of either parent. For example, a progeny plant from the *L3Lx* heterozygote gave this modified 0n reaction with rust strain B when both parents gave type 0 reaction. The progeny of this plant gave the same 0n reaction with rust strain B but surprisingly a type 4 reaction to strain C, another rust of different provenance but with the same reaction type (0) on the parents as strain B (Islam, unpublished results). We believe this observation is most significant because it could provide an explanation for the origin of new specificities at the *L* group and also it has implications for our understanding of the structure of this complex locus. However, it does not negate the hypothesis that plants with a modified type of resistance represent *cis* products of recombinations, since it is possible that the interaction leads to a new specificity. However, to prove this hypothesis it is necessary to demonstrate that both *L3* and *Lx* specificities can be recovered by rare recombination in the progeny of such plants, and these crucial tests have not yet been carried out.

Some of our findings resemble the results obtained by Wise and Ellingboe (1985) while investigating the fine structure of the *Ml-a* locus in barley conferring resistance to powdery mildew. They also obtained only susceptible recombinants from four different pairs of *Ml-a* genes, and rare resistant revertants were recovered in the progeny of the *Ml-a10/Ml-a1* susceptible recombinant. Also, the specificity of the reverants matched only one of the parents. However, their results showed some other unusual features. In one cross (*Ml-a6* × *Ml-a13*), a relatively high frequency of susceptible recombinants was observed (21 out of 8,112 F_3 families) when plants carrying *Ml-a6* were used as the female parent, but no recombinants occurred in the reciprocal cross. Moreover, they found that these recombinants were unstable and gave revertants with a resistant- or intermediate-type reaction in their progeny. They saw similarity in their results to hybrid dysgenesis in *Drosophila* caused by the P factor transposable elements (Rubin et al. 1982), and they postulated that the initial recombination in crosses between *Ml-a6* and *Ml-a13* may have been associated with a similar transposition event.

In the light of these findings with barley powdery mildew, it is of interest to consider whether transposable elements might account for some of the unusual results obtained in recombinational studies with *L* genes in flax. The occurrence of susceptible recombinants differing in their degree of susceptibility and of plants with modified type of resistance could be accounted for by the insertion of a transposon-like element into or near the *L* group, resulting in complete or partial loss of the gene product. Recovery of rare resistant plants expressing one of the parental specificities among the progeny of susceptible recombinants could then arise through excision of the transposable element. Whereas precise excision of the element would be expected to lead to normal function such as resistant revertants, imprecise excision could lead to partial or modified function such as plants with modified resistance. Wise (1983) suggested a similar phenomenon to explain the susceptible recombinant obtained among progeny of the *Ml-a1* × *Ml-a10* cross and the rare resistant revertants occurring among the progeny of that recombinant.

Although we have much genetic data revealing the complex nature of host genes in flax conferring resistance to flax rust, further understanding of their precise structure will depend on being able to clone and sequence these genes. Successful cloning of genes conferring avirulence has been accomplished (Staskawicz et al. 1984; Gabriel 1985), but prospect for using a similar approach to clone host genes conferring resistance to plant diseases are limited. However, use of transposable elements to inactivate the host resistance gene has been suggested as an alternative approach to identify the host gene product (Ellingboe 1985; Pryor 1986). Success has already been achieved in inactivating the *Rp1* gene in maize conferring resistance to its rust (Pryor 1986; Bennetzen et al. 1988). Depending on the availability of a suitable clone of the transposable element, this alternative approach offers much promise, inter alia, in flax.

In summary, the existence of a transposable element could account for many of the puzzling features observed in the present and earlier studies (Shepherd and Mayo 1972) of recombination between *L* genes in flax. However, without marker genes closely linked to the *L* group and information on the molecular basis of interactions between flax and its rust, it is difficult to obtain definitive evidence for or against the transposon hypothesis.

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