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Recessive resistance genes against potyviruses are localized in colinear genomic regions of the tomato (*Lycopersicon* spp.) and pepper (*Capsicum* spp.) genomes

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Abstract Resistance against both *Potato virus Y* (PVY) and *Tobacco etch virus* (TEV) was identified in the wild tomato relative *Lycopersicon hirsutum* PI247087. Analysis of the segregation ratio in F_2/F_3 and BC_1 interspecific progenies indicated that a single recessive gene, or two very tightly linked recessive loci, are involved in resistance to both potyviruses. This locus was named *pot-1*. Using amplified fragment length polymorphism markers and a set of *L. hirsutum* introgression lines, *pot-1* was mapped to the short arm of tomato chromosome 3, in the vicinity of the recessive *py-1* locus for resistance to corky root rot. Because of the occurrence of phenotypically similar genes in pepper (*Capsicum* spp.), the comparative genetics of resistance to potyviruses between tomato and pepper was investigated. Unlike most of the comparative genetic studies on resistance genes, *pot-1* was tightly flanked by the same restriction fragment length polymorphism (RFLP) markers than the *pvr2/pvr5* locus for resistance to PVY and TEV from pepper. These results may indicate that recessive resistance genes against potyviruses evolve less rapidly than the majority of the dominant genes cloned so far, and consequently may belong to a different family of resistance genes.

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Introduction

Compatible interaction between a virus and its host leading to a systemic infection, requires virus genome replication in the inoculated cells, cell-to-cell movement and long-distance movement through the plant vascular system (Fraser 1992). A complete or partial disruption of this process results in an incompatible interaction and can be mediated by one or several resistance factors from the host plant. Up to now, six resistance factors involved in virus resistance have been cloned; four (*N*, *Sw-5*, *Rx1* and *Rx2*) are dominant genes that trigger hypersensitive or extreme resistance and act in a "gene-for-gene" manner. They belong to the nucleotide binding site, leucine-rich repeat (NBS-LRR) super-family of resistance genes like most of the cloned genes involved in resistance to fungi, bacteria and nematodes (Whitham et al. 1994; Bendahmane et al. 1999, 2000; Brommonschenkel et al. 2000). However, all virus resistance factors do not fall into this class (Chisholm et al. 2000; Whitham et al. 2000). The two dominant genes *RTM1* and *RTM2*, involved in restriction of long-distance movement of *Tobacco etch virus* (TEV) in *Arabidopsis*, differ in that the hypersensitive response does not occur, mutants with defects in genes necessary for NBS-LRR-type resistance have no effect on TEV restriction and markers associated with systemic acquired resistance are not induced after infection by TEV. *RTM1* encodes a novel protein with repeats of a sequence found in jacalin that probably play a role in protein-protein interactions and *RTM2* also encodes for an unusual protein that shows similarities to a class of proteins with chaperone activities. Up to now, the role of these proteins in the resistance process is unknown. Equally unknown is how other types of genetically controlled virus resistance, including mainly recessive resistance genes, act to prevent virus infection.

Two hypotheses could explain the role of recessive resistance: (1) the dominant susceptibility allele encodes a factor required for the virus to replicate and/or move in the susceptible host; (2) the susceptibility allele encodes a dominant negative regulator of resistance. At present, the data about recessive resistance mainly result from the characterization of induced mutation in single host genes but none concerns virus resistance. A well-known example is the barley *mlo* mutants exhibiting broad-spectrum resistance to the powdery mildew fungus, *Erysiphe graminis* f.sp. *hordei* (Büschges et al. 1997); in this case, where naturally occurring alleles were also identified, it has been hypothesized that the corresponding wild-type gene functions as a negative regulator of resistance.

Species belonging to the *Solanaceae* family (with the three major crops tomato, pepper and potato) have been studied intensively for comparative genetic mapping and constitute a very interesting model to investigate the comparative genetics of disease resistance because numerous pathogens infect the three species and a large number of major genes and QTLs (quantitative trait loci) have been mapped and/or cloned. In contrast to genes governing morphological traits, resistance genes that confer resistance to similar or identical pathogens in different *Solanaceae* have not yet been found in colinear genomic regions (Grube et al. 2000a). This feature concerns mainly dominant genes involved in gene-for-gene interaction; indeed, only three of the 73 R-loci studied are recessive major genes: *py-1* for resistance to *Pyrenochaeta lycopersici* in tomato and *pvr1* and *pvr2* for resistance to potyviruses in pepper.

Interestingly, a higher frequency of recessive genes have been observed for potyvirus resistance (40% vs 20% for resistance against other viruses; Provvidenti and Hampton 1992) and most of these recessive genes are overcome by virulent strains. Within the *Solanaceae*, among the 16 well-characterized major resistance genes against potyviruses, eight are recessive. In pepper, at least seven major genes (named *pvr* for *p*oty*v*irus virus *r*esistance; Kyle and Palloix 1997) and several QTLs have been characterized. Genetic mapping using molecular markers allows us to identify two clusters: the first one, localized on a pepper genomic region colinear to tomato chromosome 3, includes the recessive genes *pvr1*, *pvr2* and *pvr5* and a major-effect QTL (Caranta et al. 1997; Murphy et al. 1998; Caranta, unpublished results); the second ones involves the two dominant genes *Pvr4* and *Pvr7* mapped on a pepper genomic region colinear to tomato chromosome 10 (Grube et al. 2000b). Another striking feature of the potyvirus resistance genes is that most of them are involved in resistance to two or more related potyviruses. However, general resistance against all the potyviruses infecting a single crop species was never observed.

In tomato and related species, only a few data about potyvirus resistance are available. A complete resistance to *Potato virus Y* (PVY) and TEV was identified in the *Lycopersicon hirsutum* accession PI 247087 (Légnani et al. 1995, 1996). The resistance is efficient against several PVY and TEV isolates, and both temperature and inoculum pressure do not affect its expression. In the present paper we report on the genetic analysis of the resistance to PVY and TEV and on the localization of the recessive gene *pot-1* on the tomato genome. Because of the occurrence of potyvirus resistance genes with similar phenotypes in pepper, we further investigate the comparative genetics of resistance to potyviruses between tomato and pepper. Unlike previous studies revealing that resistance to the same pathogen has not yet been found in corresponding positions among the *Solanaceae*, we provide evidence for orthology between *pot-1* from tomato and the recessive resistance gene locus *pvr2/pvr5* from pepper, indicating that they evolved less rapidly than the majority of the dominant genes studied so far.

Materials and methods

Plant materials and potyvirus isolates

The susceptible *Lycopersicon esculentum* cv Mospomorist (M) was crossed with the resistant accession *L. hirsutum* PI247087 (PI24) originating from Dr. J.E. Thomas, Queensland department of Primary Industries, Australia (Thomas 1981). F_2 seeds were obtained from a single F_1 plant. F_2 and backcross (M × F_1 and F_1 × PI24) progenies were used for preliminary determination of the number of genes involved in potyvirus resistance. Therefore, 160 F_2 plants were maintained in a greenhouse for the F_3 progeny generation and DNA extractions. Only F_3 families from which sufficient seed was obtained were assessed for PVY and TEV resistance. The recessive potyvirus resistance gene *pot-1* was assigned to a tomato chromosome by the mapping of *pot-1*-linked molecular markers on the 53 *L. hirsutum* introgression lines generated, as described by Monforte and Tanksley (2000). Most of these lines contain a single defined introgression from *L. hirsutum* LA1777 (LA17) in the *L. esculentum* cv E6203 (E6203) genetic background.

PVY isolate N-605 (isolated from *Solanum tuberosum*; Jakab et al. 1997) and TEV isolate CAA-10 (Légnani et al. 1996) were maintained according to the Bos procedure (Bos 1969) and increased on *Nicotiana tabacum* cv Xanthi nc. before inoculation to tomato plants at the two-leaf stage.

Potyvirus resistance assay

Virus inoculum was prepared as described by Légnani et al. (1995, 1996). The cotyledons and the first two leaves of tomato seedlings were mechanically inoculated. Parental lines, the F_1, F_2, BC_1 and 76 F_3 families were evaluated under growth-chamber conditions (14-h light, 18 °C night and 24 °C day) for response to mechanical inoculation with PVY-N605. Twenty four F_3 families with a clear-cut phenotype after inoculation with PVY-N605 were evaluated for response to TEV-CAA10. For both potyviruses, two independent tests on 15 plants per F_3 families were performed. Four weeks after inoculation, all plants were individually evaluated for presence/absence of PVY or TEV capsid antigen by the enzyme-linked immunosorbent assay (ELISA) as described by Légnani et al. (1995, 1996). Resistance evaluation of F_3 families allowed us to infer the F_2 genotypes as homozygous resistant (*pot-1*/*pot-1*), homozygous susceptible (*pot-1*$^+$/*pot-1*$^+$) or heterozygous (*pot-1*/*pot-1*$^+$).

DNA extraction and *pot-1* mapping

Total DNA was extracted from approximately 1 g of fresh young leaves from F_2 plants as described in Caranta et al. (1997). DNA

Table 1 Potyvirus resistance major genes mapped in *Capsicum* and tomato RFLP markers associated with each gene

Gene	Spectrum	Linked markers[b]	Chromosomal location on tomato	Reference
pvr1	TEV, PepMoV[a]	TG56, TG135	3	Murphy et al. 1998
pvr2	PVY, TEV[a]	CT31, TG132	3	Caranta et al. 1997
pvr3	PepMoV[a]	nd[c]	nd[c]	Murphy et al.1998
Pvr4	PVY, PepMoV	CD72, CT124	10	Caranta et al. 1999 Grube et al. 2000
pvr5	PVY[a]	CT31	3	Caranta, unpublished results
pvr6	PVMV	TG57	9	Caranta et al. 1996
Pvr7	PepMoV, PVY[a]	CD72, CT124	10	Grube et al. 2000

[a] Only the general resistance spectrum is indicated for each gene; some of these resistance genes can be overcome by virulent strains
[b] RFLP markers were obtained using tomato random genomic DNA (TG) or tomato leaf epidermal cDNA (CD and CT) probes
[c] nd = not determined

samples from six F_2 plants that generated F_3 families completely susceptible to PVY-N605 (F_2:*pot-1*$^+$/*pot-1*$^+$) and nine F_2 plants that generated F_3 families completely resistant to PVY-N605 (F_2:*pot-1/pot-1*) were pooled for bulked segregant analysis and AFLP tagging of *pot-1*. AFLP markers were generated using the procedure of Vos et al. (1995) with the restriction enzymes *Eco*RI, *Hin*dIII and *Mse*I. The first amplification was performed using primer combinations (PCs) with a single selective nucleotide, and the second one with PCs with three selective nucleotides. The RFLP procedure was described in Saliba-Colombani et al. (2000). Screening for polymorphism between M and PI24 was performed with three restriction enzymes (*Eco*RI, *Hin*dIII and *Xba*I) with RFLP markers previously mapped on tomato (CT, tomato cDNA derived from mRNA from tomato epidermal tissue; TG, tomato genomic DNA-clones; the probe CAB3 encodes a chlorophyll a/b binding polypeptide, Tanksley et al. 1992) to map additional markers on chromosome 3 and to perform comparative genetic analysis with pepper.

Segregation analysis for molecular markers (AFLPs and RFLPs) and resistance data was performed with the Mapmaker/Exp v. 3.0 software with a minimum LOD score of 4.0 and a maximum recombination fraction of 0.3. Recombination fractions were converted into map distances in centiMorgans (cM) using the Kosambi mapping function (Kosambi 1944).

Mapping potyvirus resistance genes in pepper

Five major genes and several QTLs involved in potyvirus resistance were mapped on the pepper genome. Thanks to the use of common RFLP probes for genome mapping and the strong conservation of marker order between the tomato and the pepper genome, pepper potyvirus resistance factors were placed on the tomato map. Tomato chromosomal location of pepper potyvirus resistance loci together with the linked RFLP markers are listed in Table 1. In order to state precisely the correspondence between pepper and tomato genomic regions with potyvirus resistance genes, the RFLP markers TG135, CAB3 and CT31 were added to the pre-existing pepper genetic linkage maps (Lefebvre et al., in press).

Results

Identification of a recessive gene for potyvirus resistance in *L. hirsutum*

Evaluation of resistance to PVY and TEV was performed by the ELISA assay of non-inoculated tissues of the parental lines *L. esculentum* Mospomorist (M) and *L. hirsutum* PI247087 (PI24), the F_1 hybrid, F_2 and BC_1 progenies and F_3 families, 28 to 30 days post-inoculation. The parental line M and the (M × PI24)F_1 hybrid were susceptible to PVY-N605 and TEV-CAA10, presenting coat-protein (CP) accumulation in non-inoculated tissues similar to the susceptible control (data not shown), whereas PVY and TEV-CP were never detected in tissues from the resistant line PI24. In accordance with previous studies (Légnani et al. 1995, 1996), these results demonstrated that PVY and TEV resistance in PI24 are inherited as recessive traits.

The response of F_2 and BC_1 progenies to inoculation with PVY-N605 demonstrated segregation ratios consistent with monogenic recessive inheritance of resistance (Table 2). When 76 F_3 families were screened with PVY-N605, 11 families were completely susceptible, indicating that the original F_2 were homozygous susceptible, 19 were completely resistant, indicating that the original F_2 were homozygous resistant, and 46 segregated 3S:1R, demonstrating that the original F_2 was heterozygous. Analysis of the segregation ratio indicated an acceptable fit to the Mendelian segregation of a recessive gene in a completely classified F_2 progeny (Table 2). For all segregation analysis on F_2, BC_1 and F_3 progenies, we observed a higher than expected number of *L. hirsutum* homozygous genotypes (i.e. resistant plants). Segregation distorsions in favor of the wild species were previously described in progenies derived from interspecific crosses between cultivated tomato and *L. hirsutum*, and was at least partially explained by gametophytic selection (Helentjaris et al. 1986). The single recessive gene associated with PVY-N605 resistance from *L. hirsutum* PI24 was designated *pot-1* for *pot*yvirus resistance, the first characterized locus in tomato.

PI24 resistance to TEV was previously described to be under the control of a single recessive gene (Légnani et al. 1996). To determine whether recessive resistance to PVY and TEV in *L. hirsutum* are linked, a subset of 24 F_3 families already characterized for PVY-N605 resistance were inoculated with TEV-CAA10. All 24 families showed complete agreement between the PVY-N605 and TEV-CAA10 resistance genotypes (ten were completely

Table 2 Inheritance of PVY-N605 resistance in *L. hirsutum* PI247087

Genotype	Phenotype		Expected ratio	χ^{2a}	P[a]
	R	S			
L. esculentum Mospomorist (M)	0	20	0:1	–	–
L. hirsutum PI247087 (PI24)	20	0	1:0	–	–
(M × PI24)F_1	0	20	0:1	–	–
(M × PI24)F_2	31	69	1:3	1.92	0.17
(M × PI24)F_1 × PI24	38	27	1:1	1.86	0.17
M × (M × PI24)F_1	0	87	0:1	–	–
	Phenotype of 30 plants/F_3				
	R[b]	1R:3S[c]	S[d]		
(M × PI24)F_3	19	43	11	1:2:1	5.05	0.08

[a] The χ^2 and *P*-values result from a chi-square test of fit of the data to a single recessive gene model (1R:3S for the F_2, 1R:1S for the BC_1R and 1R:2Ht:1S for the F_3 families)
[b] The 30 plants of the F_3 family were all resistant (R) indicating that the parental F_2 was homozygous resistant (*pot-1/pot-1*)
[c] A ratio of 1R:3S was observed among the 30 plants of the F_3 family indicating that the parental F_2 was heterozygous (Ht, *pot-1+/pot-1*)
[d] The 30 plants of the F_3 family were all susceptible (S) indicating that the parental F_2 was homozygous susceptible (*pot-1+/pot-1+*)

resistant, 11 were heterozygous and three were completely susceptible to both PVY and TEV), indicating that the gene(s) does (do) not segregate independently. Either two linked genes or a single locus therefore control PVY and TEV resistance in PI24.

AFLP mapping of the resistance locus

A DNA pooling strategy based on phenotypic information available from the F_2/F_3 progenies was used to identify AFLP markers linked to *pot-1* (Michelmore et al. 1991). The two DNA pools were made with DNA from six homozygous-susceptible F_2 plants and with DNA from nine homozygous-resistant F_2 plants. A total of 126 selective primer combinations (PCs) was tested on the two DNA pools and the two parents. Two fragments amplified using *Eco*RI-AAA/*Mse*I-CAC and *Eco*RI-AAA/*Mse*I-CAG PCs with a clear polymorphism between the resistant and the susceptible pools were detected and mapped on the F_2 progeny. The resistance gene *pot-1* was shown to be flanked on both sides by the two AFLP markers (1.2 and 4.7 cM from *pot-1*, respectively, Fig. 1A).

Analysis of introgression lines indicates that *pot-1* maps on tomato chromosome 3

A population of 53 introgression lines (IL) obtained from the cross between LA17 and E6203 was used to narrow-down the position of the *pot-1* gene. This was feasible because polymorphic amplified fragments generated using *Eco*RI-AAA/*Mse*I-CAC and *Eco*RI-AAA/*Mse*I-CAG PCs with exactly the same molecular weight were observed between PI24/LA1777 (no amplification) and M/E6203 (amplification of the fragments). When the ILs

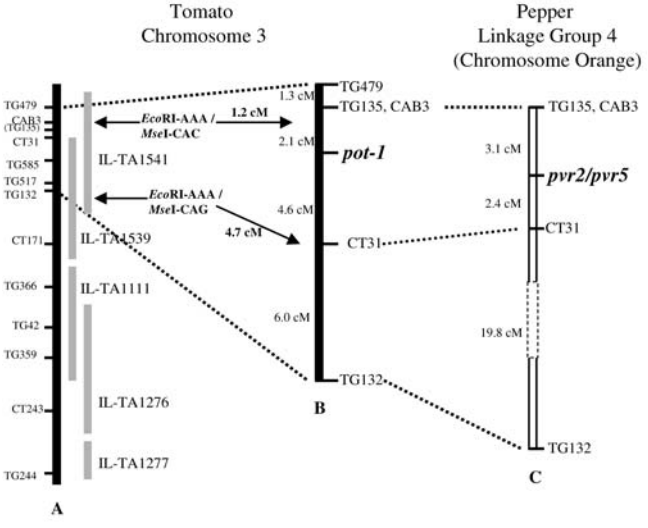

Fig. 1 Map location of the *pot-1* resistance gene on tomato chromosome 3 and comparative mapping with the *pvr2*/*pvr5* locus from *C. annuum*. *A* represents the marker order on tomato chromosome 3 as determined by Tanksley et al. (1992). Introgression fragments from chromosome 3 of *L. hirsutum* (Montforte and Tanksley 2000) are superimposed on the map, together with the two AFLP markers (localized on ILs using *arrows*) linked to *pot-1* and detected using bulked segregant analysis. *B* represents the marker order around the resistance gene *pot-1* in the F_2/F_3 progeny derived from the (PI24 × M)F_1 as determined by Mapmaker. The position of AFLP markers is indicated by *arrows* together with the distance in cM from *pot-1* estimated in the F_2/F_3 progeny. *C* shows the linkage between the RFLP markers TG135, CAB3, CT31, TG132 and the *pvr2*/*pvr5* locus. The alignment of markers between *A*, *B* and *C* is indicated by *dotted lines*

were screened for the two *pot-1* linked markers, only one line, IL-TA1541, presented polymorphism with the *Eco*RI-AAA/*Mse*I-CAC PC (Fig. 2), and two lines, IL-TA1541 and IL-TA1539, with the *Eco*RI-AAA/*Mse*I-CAG PC. Both IL-TA1541 and IL-TA1539 carried over-

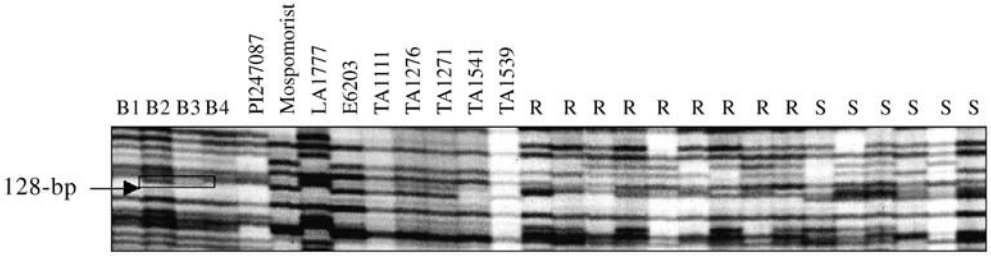

Fig. 2 Cosegregation of susceptibility to *Potato virus Y* (PVY) in tomato with the 128-bp amplification product from primer combinations *Eco*RI-AAA/*Mse*I-CAC. The size of the fragment was determined using the ϕX174RF DNA-*Hinc*II Digest ladder from Pharmacia. The 128-bp amplification product is present in the susceptible *L. esculentum* lines M and E6203, in the susceptible F_2 DNA-pool (*lanes B2 and B3*, surrounded) and in the six F_2 individuals from the susceptible DNA pool (*lanes S*). The 128-bp fragment is absent in the *L. hirsutum* lines PI24 and LA17, in the resistant F_2 DNA pool (*lanes B1 and B4*) and in the nine F_2 individuals from the resistant DNA pool (*lanes R*). Among the five introgression lines with overlapping segments of tomato chromosome 3 (*TA1111, TA1276, TA1271, TA1541 and TA1539*, Montforte and Tanksley 2000), only *TA1541* is lacking the 128-bp fragment, indicating that it maps on this chromosome segment

lapping fragments from chromosome 3 of *L. hirsutum* (Fig. 1B; Monforte and Tanksley 2000).

To see whether the identical size of the AFLP fragment (linked to *pot-1*) between *L. hirsutum* PI24 and LA1777, and between *L. esculentum* M and E6203, correspond to the same locus and consequently confirm the map location of *pot-1*, five RFLP markers mapped on the short arm of chromosome 3 (Tanksley et al. 1992) were analyzed in the (M × PI24)F_2/F_3 progeny segregating for *pot-1*. Linkage analysis revealed that *pot-1* is linked to all markers, and flanked by CAB3 and TG135 on one side, and CT31 on the other side (2.1 and 4.6 cM, respectively; Fig. 1A and B).

Comparative mapping with phenotypically similar resistance genes from pepper

To examine the correspondence between the genomic position of *pot-1* from tomato and phenotypically similar genes from pepper, tomato probes CAB3, TG135 and CT31 linked to *pot-1* were added to the *Capsicum annuum* intraspecific maps segregating for *pvr2* or *pvr5*. The three markers were found to group with pepper linkage group 4 (corresponding to the chromosome Orange) in a genomic region colinear with the short arm of tomato chromosome 3, and were also flanking the *pvr2/pvr5* locus (3.1 and 2.4 cM, respectively; Fig. 1C).

Discussion

Segregation analysis of BC_1 and F_2/F_3 progenies obtained from the interspecific cross between *L. esculentum* and *L. hirsutum* indicated that a single recessive gene, tentatively named *pot-1*, is involved in PVY resistance. Further characterization of F_3 families for another potyvirus resistance showed that the recessive gene controlling resistance against the TEV does not segregate independently from *pot-1*. As proposed in Kyle and Palloix (1997), a single symbol was attributed to the resistance to the two potyviruses, since there is no evidence to-date that distinct factors are involved. All these results are consistent with features that we, and others, have observed in most of the plant-potyvirus interactions: the frequent occurrence of recessive resistance factors (major genes and QTLs) and the cosegregation of resistance to several related potyviruses (Kyle and Provvidenti 1993; Brigneti et al. 1997; Caranta et al. 1997; Hämäläinen et al. 1997).

Introgression lines of the *L. hirsutum* genome in a *L. esculentum* background (Montforte and Tanksley 2000), together with the locus specificity of AFLP markers among the *L. hirsutum* accessions LA17 and PI24, allowed us to localize the *pot-1* locus on the short arm of tomato chromosome 3 in the vicinity of the RFLP markers TG135, CAB3 and CT31. Among the some 40 disease resistance loci mapped on the tomato genome, only one except *pot-1* is recessive. This is the *py-1* locus from *L. peruvianum* involved in resistance to corky root rot (Doganlar et al. 1998). Interestingly, *py-1* was also located on the short arm of tomato chromosome 3, within the same 10-cM interval than *pot-1*. This grouping defines the first such cluster of recessive resistance loci in tomato. Whether the occurrence of these two genes in the same cluster reflects shared components involved in plant-pathogen interactions remains to be determined, but it is striking that the two recessive resistance genes mapped on the tomato genome were localized in the same cluster.

Genetic mapping of the *pot-1* locus allowed us to examine the possibility of evolutionary relationships with a phenotypically similar gene from pepper. Among the potyvirus resistance genes mapped on the pepper genome (Table 1), we focussed on the *pvr2/pvr5* locus because it shares strong similarities with *pot-1*: both are recessive loci involved in resistance to both PVY and TEV. The resistance mechanism controlled by *pvr2* varies from restriction of cell-to-cell movement to inhibition of viral coat protein accumulation (Arroyo et al. 1996; Deom et al. 1997; Murphy et al. 1998). Similarly, PVY was not detected in the inoculated leaves of *pot-1* plants using ELISA tests and back-inoculation on susceptible hosts, suggesting that virus multiplication and/or cell-to-

cell movement is impaired (unpublished results). Both genes are overcome by virulent PVY and TEV strains. In order to complete the comparison between *pot-1* and *pvr2*, and to shed light on the *Solanaceae*-Potyvirus interaction, the resistance-breaking mutations in both PVY and TEV are under study (Morel et al. 2000).

The results we obtained in this study *via* comparative genetic mapping between tomato and pepper clearly showed that *pot-1* and *pvr2* are localized in a colinear genomic region, within the same 5–6 cM. To our knowledge this is the first demonstration of colinearity between two phenotypically similar recessive resistance genes. Indeed, the systematic review of all known map positions for resistance genes revealed that resistance (mainly dominant genes) to the same pathogen has never been observed in corresponding positions, even if transgenic expression of resistance genes in heterologous solanaceous species suggests that most of the components required for the resistance response are conserved (Grube et al. 2000a). Examples are the *Sw-5* and the *Tsw* genes from tomato and pepper conferring resistance to the *Tomato spotted wilt virus*, and the *Tm-2*, *L* and *N* genes from tomato, pepper and tobacco, respectively, conferring resistance to the *Tobacco mosaic virus*. Despite their phenotypic and genetic similarities, these loci do not appear to share a recent common evolutionary ancestor (Jahn et al. 2000; Caranta, unpublished results). Likewise for potyvirus resistance, the dominant genes *Pvr4* and *Pvr7* from pepper are similar in both inheritance and resistance phenotype to a cluster of potyvirus resistance loci in *Solanum* (Ry_{sto}/Ry_{adg}, Na_{adg}), but comparative mapping results suggest that these clusters are not orthologous (Grube et al. 2000b). The *Sw-5* and *N* genes belong to the NBS-LRR super-family of resistance genes (Whitham et al. 1994; Brommonschenkel et al. 2000). Possible explanations for this absence of synteny are: (1) the recent reports indicating that the sequences of some LRR-type of resistance gene are particularly subject to rapid evolution and that regions of the LRR proteins implicated in recognition specificity are affected by diversifying selection (Michelmore and Meyers 1998; Caicedo et al. 1999), and (2) the fact that these resistance genes may target different avirulence genes from the pathogen. Taken together, these data illustrate the complexity of this topic.

In fact, there is only one reported case among plant resistance genes where resistance to the same pathogen has been attributed to evolutionary related loci in a distinct genus: this concerns the dominant *Hm-1* and *Hm-2* loci from maize conferring resistance to *Cochliobolus carbonum*. Sorghum and rice are also resistant to the disease and *Hm-1* and *Hm-2* homologs were mapped to two chromosomal regions from sorghum and rice that are syntenic with the maize *Hm-1* and *Hm-2* loci (Multani et al. 1998). These genes were shown to encode a toxin reductase that corresponds to the resistance function; thus, they are unrelated to the resistance genes cloned so far, acting in a "gene-for-gene" manner. The results we obtained in this study may indicate that the *pvr2/pot-1*-encoded resistance is of ancient origin (and should be conserved among all the *Solanaceae*), and that the susceptible/resistant alleles correspond to a general and constitutive susceptibility/resistance function instead of a molecular determinant of recognition, triggering an induced resistance. This is in agreement with the generally admitted hypothesis concerning recessive virus resistance genes, i.e. the resistant host is lacking a function essential for particular steps in viral infection (Fraser 1992). In order to validate this hypothesis, we have begun the molecular characterization of these recessive resistance factors. As the different alleles and QTLs located at the *pot-1/pvr2* locus display various levels of specificity towards potyviruses and potyvirus strains, it will provide keys to further understanding of the components of broad-spectrum resistance versus specific resistance and, consequently, tools to design genes controlling resistance with a high level and increased durability.

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