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QTLs for resistance to powdery mildew in pepper under natural and artificial infections

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Abstract Epidemics of powdery mildew due to *Leveillula taurica* is an increasing problem in pepper production areas, particularly in coastal regions or greenhouse cultivation. The highly resistant genitor 'H3' was submitted to genetic analysis and QTL mapping in order to promote the introgression of its oligogenic resistance into large and sweet-fruited cultivars. The doubled-haploid progeny from the cross 'H3' (resistant) by 'Vania' (susceptible) was tested for resistance under both natural field infection and artificial inoculation tests, and QTL detection was compared for those two methods. Seven genomic regions including additive QTLs and epistatic interactions were detected, explaining altogether the major part of genotypic variance. Two genomic regions were common to both the evaluation methods, whereas other QTLs were method-specific, reflecting the environment dependence of powdery mildew epidemics. Orthologies with tomato genomic regions carrying resistance genes to *L. taurica* and *Oidium lycopersicum* were revealed by comparative mapping with pepper. Tight linkages between the detected QTLs and virus resistance or fruit color traits in pepper were also shown, which adds to the agronomic importance of these regions in pepper breeding programs.

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Introduction

Powdery mildew caused by *Leveillula taurica* was known as a significant pathogen infecting pepper and other vegetable crops for a long time (Palti 1971). Since the early 1990s, growers, pathologists and breeders more and more report on cases of epidemics caused by this fungal parasite in greenhouses and in open fields, in most of the pepper production areas. Premature leaf shed caused by the disease strongly affects production and makes fruits unmarketable. Whereas most powdery mildews are ectoparasites, the mycelium from *L. taurica* grows intercellularly within the host tissues limiting the chemical control efficiency. Very little literature is available concerning pepper resistance to *L. taurica*. Accessions exhibiting various resistance levels in natural infection conditions were reported in different *Capsicum* species including *Capsicum annuum, Capsicum baccatum* and *Capsicum chinense* (Ullasa et al. 1981; Desphande et al. 1985; Pochard et al. 1986). The most promising source of resistance was found in the small-fruited and pungent *C. annuum* accession 'H3' from East Africa (Daubèze et al. 1989). Its level of resistance was shown to be stable in many cultivation areas including France, Italy, Israel and Tunisia (Shifriss et al. 1992; Allagui et al. 1995; Daubèze et al. 1995a), and its intraspecific origin should facilitate the transfer of the resistance to large and sweet-fruited varieties. Quantitative genetic analyses further concluded that three to five genetic factors with significant epistatic effects were involved in the resistance under severe infection conditions (Daubèze et al. 1995a; Murthy and Deshpande 1997). Up to now, selection for resistance was performed under natural infection conditions. Two main components where shown to characterise the resistant accessions: the sporulation intensity and the proportion of infected leaves (Daubèze et al. 1995a). Environmental conditions such as temperature and moisture greatly affect

the epidemics and hamper the breeding for this trait. An artificial inoculation test performed in a growth chamber was recently set up for accelerating and controlling the screening method (Daubèze et al. 1995b).

Research on molecular markers linked to the resistance genetic factors for powdery mildew was performed to state precisely the genetic knowledge of this economically valuable trait and to promote marker-assisted breeding programs. In this paper, we report a genetic analysis of resistance to powdery mildew from the H3 inbred line using both field evaluations under natural infection and growth chamber evaluations under artificial infection. QTL analysis revealed two QTLs detected in both infection conditions and other QTLs specific to evaluations methods. Comparative mapping for disease resistance was investigated within *Capsicum* and with other Solanaceaous crops.

Materials and methods

Plant material and genetic map

H3, the powdery mildew resistant genotype, is a pungent small-fruited *C. annuum* inbred line obtained from an Ethiopian accession (Daubèze et al. 1995a). Vania is a susceptible bell-pepper inbred line from INRA. A total of 101 doubled haploid lines (HV population) were obtained from the (H3 × Vania) F1 hybrid, using the androgenesis method described by Dumas de Vaulx et al. (1981). A molecular map was obtained from this population including 553 molecular markers with a minimum LOD score of 5.0 and a maximum recombination fraction of 0.3 as thresholds for linkage detection (Lefebvre et al. 2002). A set of 134 well-distributed markers (1 phenotypic, 32 RFLP, 27 RAPD and 74 AFLP markers) constituted the framework map. They were distributed on 20 linkage groups spanning a total map length of 1,513 Haldane cM, with an average inter-marker distance of 12.9 cM (SD: ±8.7 cM). As a result of alignment with other pepper maps, 16 linkage groups were assigned to the 12 pepper chromosomes.

Pathogen material and assessment of powdery mildew resistance

The HV population was evaluated for resistance to powdery mildew using field evaluations under natural infection conditions during 2 years (1999 and 2000) in a single location (Montfavet, France). Two independent field trials, consisting of two randomised complete blocks composed of three plants per genotype, were evaluated for resistance as soon as the susceptible control Vania was heavily infected, about 4 months after field plantation. Two resistance components were assessed on each plant, as described by Daubèze et al. (1995a): the proportion of infected leaves per plant (PrF) on a scale from 0 = no infected leaves to 5 = the whole foliage infected, and the sporulation intensity on infected leaves (SpF) on a scale from 0 = no visible sporulation to 5 = the whole surface of the leaf covered with dense sporulations. A synthetic disease index (DIF) was obtained by summing the two components: DIF = PrF + SpF. Values of PrF, SpF and DIF were averaged for each DH line and for both years of experiment (indicated in Tables 1 and 2 by PrF99, PrF00, SpF99, SpF00 and DIF99, DIF00 respectively), and used in further analyses.

Two independent artificial resistance tests (T1 and T2) were performed on a single plant of 52 DH lines randomly sampled in the HV population. The moderately aggressive strain P38 was isolated from infected pepper leaves in a field in Sicily (Italy) and was single-spored. Maintenance of isolate and inoculum production were carried out on *Lagenaria leucantha* cv Minibottle (Takii Seeds) cotyledons, according to the method derived from Molot et al. (1990) and Daubèze et al. (1995b). Spore suspension of *L. taurica* was prepared according to the method described by Suliman et al. (1999) and adjusted to 10^5 spores/ml. The lower surface of the two first leaves of four-leaf stage pepper plants decapitated below the 3rd leaf was sprayed with 1-ml of the conidial suspension (1 ml/plant). Plants were arranged in the growth chamber in a randomised design and plant position was changed every week to avoid border effects. Immediately after spraying, plants were maintained in darkness during 24 h at 16 °C, then submitted to daily cycles of 14-h of light at 22 °C and 10-h of darkness at 16 °C. During the first 48 h, relative humidity (rH) was maintained at 100%, then conditions were adjusted to 60% rH during light period and 100% rH during darkness. Sporulation intensity (Sp) in both tests (indicated in Tables 1 and 2 by SpT1 and SpT2 respectively) was assessed on the lower face of inoculated leaves according to a scale from 0 (no visible sporulation) to 5 (whole leaf surface covered with sporulation). Notations were done seven times at weekly intervals from the 1st week after inoculation to the 7th-week after inoculation. This last evaluation was taken into account for further analyses.

Data analysis

Genotypic effects and heritabilities of the genotypic mean values were calculated from the ANOVA analysis results as described by Lefebvre and Palloix (1996). QTL detection was performed using linear regression (LR), simple interval mapping (IM) and composite interval mapping (CIM) with the QTL Cartographer software (Basten et al. 1997) on the mean values of each DH line. A maximum of five markers, selected by a forward-backward stepwise regression analysis, was used as cofactors in the CIM procedure, with a window size of 10 cM and a walking speed of 2 cM. Significance thresholds were computed for IM and CIM by 1,000-permutation tests. No major differences of empirical thresholds were observed among traits. The LOD threshold values of 2.59, 2.40 and 2.60 were employed for LR, IM and CIM, respectively (for a type-I-error $\alpha = 0.1$). Digenic interactions between markers of the framework map were tested using a two-way analysis of variance with an interaction component (GLM procedure of SAS, 1989) as described by Lefebvre and Palloix (1996). Significant epistasis was retained when $P < 10^{-5}$. Magnitude of the marker(s)-associated phenotypic effect is described by the coefficient of determination of the model (R^2).

Results

Inheritance of the resistance and trait correlations

Parental, F1-hybrid and HV-population mean values for the eight quantitative traits analysed are presented in Table 1. The F1-hybrid always showed intermediate values between the two parent means indicating incomplete dominance of the resistance response. Analysis of variance of each variable revealed that the genetic variance was highly significant ($P < 0.0001$) which means that all resistance components assessed had a genetic basis. "Block" and "block × genotype" effects in the field for the 2-year evaluations are slightly significant compared to the genetic effect. Heritabilities, listed in Table 1, indicate that phenotypic variation was barely affected by environmental factors, giving evidence for the reliability of field evaluations. HV population distributions (data not shown) were continuous. No qualitative

Table 1 Mean and heritabilities of the resistance components to powdery mildew in the parental, F1 and HV generations

Trait	H3	Va	F1	Mean HV (SD)	W[a] (Pr > W)	h^{2b}
PrF99	0.33	4.50	3.00	2.94 (1.20)	0.8974 (<0.0001)	0.75
SpF99	0.17	3.56	1.67	2.00 (1.07)	0.9776 (0.0829)	0.72
DIF99	0.50	8.06	4.67	4.94 (2.17)	0.9674 (0.0133)	0.78
PrF00	0.00	4.80	3.33	2.50 (1.59)	0.8837 (<0.0001)	0.84
SpF00	0.00	5.00	2.00	1.88 (1.45)	0.9290 (<0.0001)	0.83
DIF00	0.00	9.80	5.33	4.37 (2.97)	0.9368 (0.0001)	0.86
SpT1	0.00	4.83	1.75	1.73 (1.71)	0.8496 (<0.0001)	–
SpT2	0.00	3.90	n.a.[c]	1.06 (1.52)	0.7189 (<0.0001)	–

[a] W is the Shapiro and Wilk's test value, and Pr > W indicate the probability associated to the Normality test
[b] h^2 is the heritability of the test
[c] n.a.: not available

Table 2 QTLs for powdery mildew resistance detected in the HV progeny

QTLs with additive effect (detected by CIM)

Trait	QTL	Chrom.	Marker[a]	Position[b]	LOD value	R^{2c}	Resistant allele	Additive effect
PrF99	*Lt_6.1*	P6	E36/M59-380h	90.82	9.0778	0.2598	H	1.2682
SpF99	*Lt_6.1*	P6	E36/M59-380h	90.82	3.3966	0.1102	H	0.7387
DIF99	*Lt_6.1*	P6	E36/M59-380h	90.82	7.1651	0.2141	H	2.0794
PrF00	*Lt_6.1*	P6	E36/M59-380h	90.82	3.3989	0.1175	H	1.1117
	Lt_9.1	P9	D11_0.8h	25.24	3.3106	0.1165	H	1.4785
DIF00	*Lt_6.1*	P6	E36/M59-380h	90.82	2.7338	0.0941	H	1.8501
	Lt_9.1	P9	D11_0.8h	25.24	3.6763	0.1315	H	2.9317
SpT1	*Lt_5.1*	P5	TG483	23.79	3.5871	0.1348	V	–1.4045
	Lt_6.1	P6	E36/M59-380h	90.82	3.8013	0.1964	H	1.6302
	Lt_10.1	P10	E38/M61-414v	0.01	3.2782	0.1648	H	1.4436
SpT2	*Lt_5.1*	P5	TG123v	24.31	3.6199	0.1789	V	–1.3996
	Lt_12.1	P12	P14/M62-254h	21.18	3.4030	0.1607	H	1.2946

QTLs with epistatic effect (detected by two-way ANOVA with an interaction factor)

Trait	Chrom.	Markers	Prob. (epistasis)	R^2	The more-resistant allele interaction
SpF99	P5 * P10	H05_1.3 * E40/M48-241v	7.49E-06	0.2232	V-V
DIF00	P2 * HV1	P14/M50-080v * P11/M54-159h	6.89E-06	0.2899	H-H

[a] Marker indicates the nearest upper flanking marker to QTL
[b] Position is the position of the QTL from the upper part in Morgans
[c] R^2 is the proportion of variance explained by a QTL at the test site or by the interaction between two markers (epistasis)

inheritance can be detected. Shapiro and Wilk's values (Table 1) moderately deviate from the Normality criteria, particularly for variables issued from the artificial tests that are skewed toward resistance.

Significant Pearson's correlations were detected between resistance components. They ranged from $r = 0.83$ to $r = 0.97$ for components assessed within a field evaluation, and from $r = 0.62$ to $r = 0.76$ between both the field evaluations for the different components. Both the artificial tests were highly significantly correlated ($r = 0.82$, p value $= 1.7 \times 10^{-13}$). Correlations between field evaluations and artificial tests were lower ranging from $r = 0.43$ to $r = 0.68$ but significant (p value $< 10^{-2}$).

Mapping of resistance loci

Five genomic regions distributed on five distinct chromosomes were involved in the quantitative resistance to powdery mildew, ranging from 0 to 3 QTLs per trait (Table 2, Fig. 1). QTLs were named by two letters indicating the considered parasite (*Lt* for *L. taurica*), followed by one digit indicating the carrier chromosome and a number to facilitate further nomenclature on the same chromosome. When several linked markers were significantly associated with the resistance, we considered the overall region as a single QTL. QTL results did not significantly differ using the three detection methods: LR, IM and CIM. QTLs on P5, P6 and P10 detected by ANOVA and IM, were also significant with CIM. The CIM method detected two additional QTLs on P9 and P12. Because of the precision of the CIM method

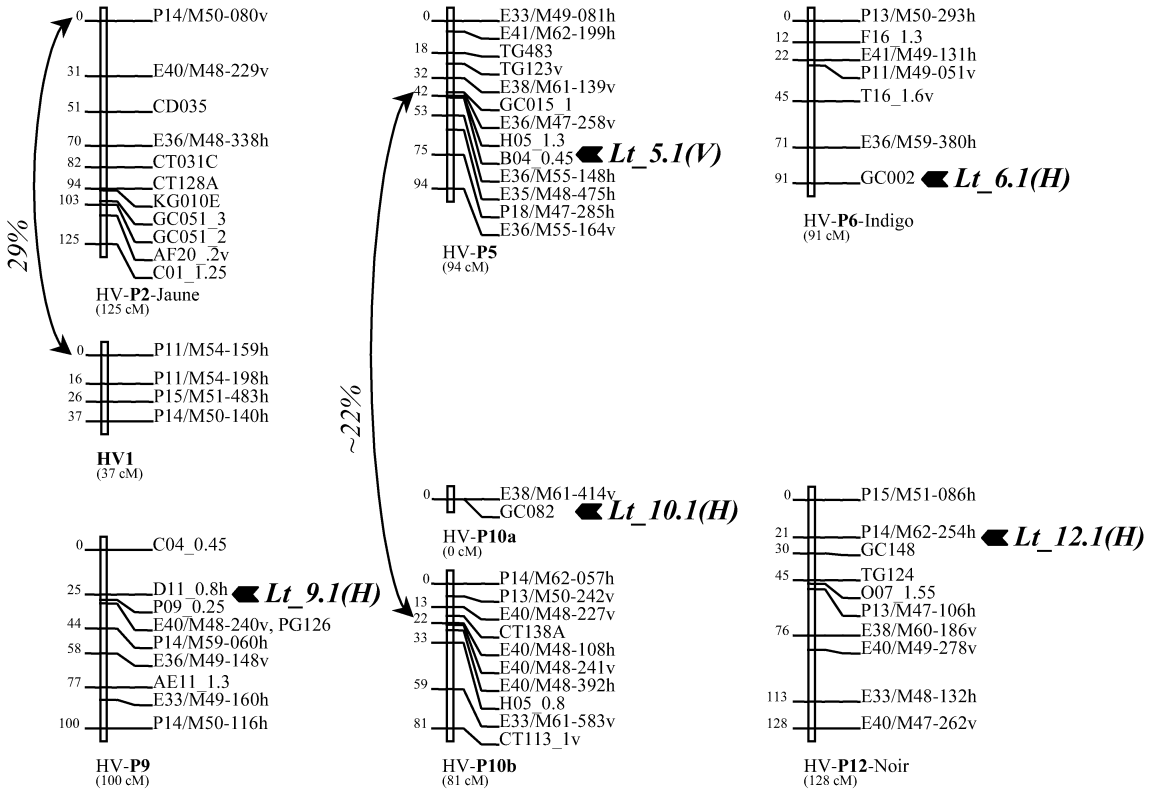

Fig. 1 Map location of powdery mildew resistance QTLs on the HV map. Only linkage groups holding QTLs associated with the resistance to *L. taurica* are shown. *Marker names* refer to Lefebvre et al. (2002). Distances in centiMorgans are to the *left* of each linkage group. The large arrows to the *right* of linkage groups indicate the position of the additive effect QTLs, and the *curved arrows* indicate digenic interaction between loci involved in powdery mildew resistance

regarding the QTL position and the R^2 evaluation (Zeng 1994), we choose to present CIM results only (Table 2). Using both field evaluations and artificial tests, a consistent QTL, named *Lt-6.1*, was detected for most of the variables analysed. It explained between 9.4% and 26.0% of the phenotypic variation depending on the year of evaluation, the resistance component and the evaluation method. The LR and IM methods detected the QTL *Lt-10.1* with PrF99, DIF99 and SpT1, whereas the CIM method associated this region only to SpT1 with R^2 = 16.5%. The QTL *Lt-9.1* is specific of the 2000-field evaluation and displays a lower effect on the resistance (R^2 = 11.6 to 13.1%). Two additional QTLs, specific to artificial tests, were detected: *Lt-5.1* detected with the two independent tests explained 13.5 to 17.9% of the observed variation, and *Lt-12.1* was only detected for SpT2 with R^2 = 16.1%. For most of the QTLs, the resistant parent H3 allele contributed to an increased level of resistance, whereas for *Lt-5.1* the Vania allele increased the resistance response.

Two-way ANOVA with an interaction effect allowed the detection of two significant epistatic effects ($P < 10^{-5}$), between P5 and P10 on the one hand, and between P2 and the unassigned linkage group HV1 on the other hand (Table 2). The first one involved a marker close to the additive effect QTL *Lt-5.1* and another marker on the chromosome bearing *Lt-10.1*. It explained 22.3% of the SpF99 variation. The highest level of resistance was observed when the two alleles originating from the same parent are present (Fig. 2a). This interaction was also detected for DIF99 and for field evaluations in Sicily, Italy (data not shown), but the significance level was slightly below the threshold ($P = 4, 1 \times 10^{-5}$). The second epistatic interaction involved two chromosomal regions without a significant additive effect. It explained 29.0% of the DIF00 variation. It was also very close to the significance threshold for other variables (PrF00, SpF00) and for belated field evaluations (data not shown). The combination of the H3 alleles at both the loci was associated with a higher level of resistance (Fig. 2b).

Multiple regression revealed that the five additive QTLs detected explained up to 37.7% and 18.0% of the phenotypic variance of field assessments in 1999 and in 2000, respectively, and up to 62.5% of the phenotypic variance of the artificial test assessments. Combining this model with the digenic interaction between P2 and P5 increased the R^2 up to 44.8% for DIF00 and up to 64.7% for SpT1. Taking into account heritability values, both the additive and epistatic QTLs detected explained together more than 50% of the genetic variation.

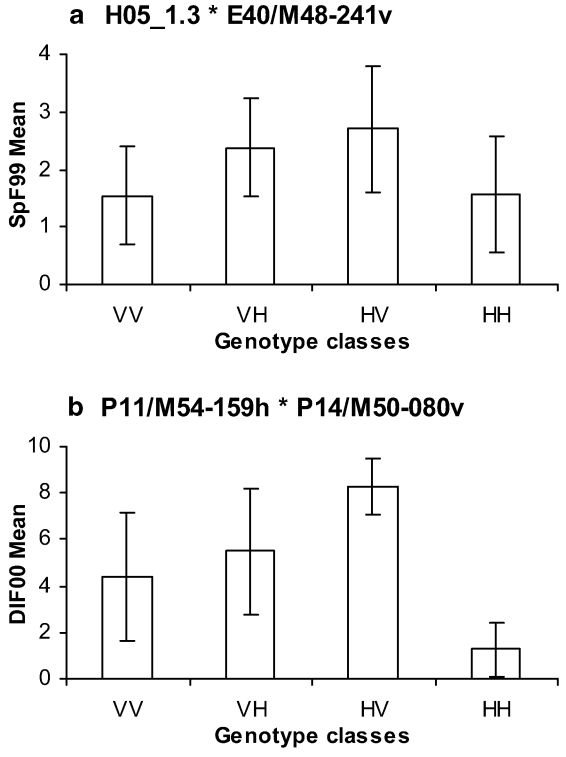

Fig. 2a, b The effect of interaction between two markers on the powdery mildew resistance components. *Bars* represent the phenotypic mean with standard deviation for each of the marker classes in the digenic interaction. **a** Interaction between H05_1.3 * E40/M48-241v. **b** Interaction between P11/M54-159h * P14/M50-080v. HH, VH, HV and VV represent the four genotype-combinations at the two loci (with H for the H3 allele at the marker and V for the Vania allele at the marker)

Discussion

To our knowledge, this study is the first report identifying QTLs associated with the powdery mildew resistance in pepper. Additive QTLs were located on five chromosomal regions on P5, P6, P9, P10 and P12. Looking for epistatic effects enabled us to detect two more regions: on P2 and on the unassigned linkage group HV1. The P6 chromosome contained the most consistent QTL; it was detected for six out of eight traits that were assessed by field as well as by artificial evaluations and it displayed the main effect (up to 26% of the total phenotypic variation). No QTLs were associated with a particular resistance component, probably resulting from their high correlation. Incomplete correspondence between the 2-year evaluations may result from different populations of *L. taurica* or/and different environmental conditions between the 2 years. If the overall resistance phenotype was shown to be stable in different areas and years (Daubèze et al. 1995a), expression of the individual QTLs may display specificities (Caranta et al. 1997). This strengthens the utility to evaluate resistance during several years and in different locations to evaluate the individual effect of QTLs. Similarly, three QTLs (localized on P5, P10 and P12) were associated with artificial evaluations only. It is noted that for the 1999-field-evaluation, the QTL on P10 was just below the threshold, and that the QTL on P5 was involved in an epistatic effect. The combination of all QTLs explained more than 50% of the genotypic variance. These results confirm the previous phenotypic analyses (Daubèze et al. 1995a) indicating that three to five genetic factors were involved in the segregation observed in field infection, and that significant epistatic effects were revealed in heavy infection conditions.

The artificial tests were less severe than the natural field infections. They permitted us to detect the effect of the *Lt6.1*, but also minor effect QTLs that were not detected through field evaluations. Only 52 of the 101 DH lines were submitted to artificial testing, that may explain the observed differences. However, powdery mildew epidemics require specific environmental conditions (Palti 1971), and artificial testing required a stringent control of light, temperature and relative humidity, thus condition-specific QTLs may also occur, particularly for the *Lt-9.1* and *Lt-12.1* QTLs.

Using common RFLP markers, comparative mapping of the HV map with the tomato map (Tanksley et al. 1992) indicated putative functional colinearities. The marker PG126 linked to the QTL *Lt-9.1* is closely linked to CT100 in other pepper maps (Lefebvre et al. 2002), and this marker was linked to the *Lv* locus on tomato chromosome 12, controlling the resistance to *L. taurica* (Chungwongse et al. 1997). Consequently, *Lt-9.1* is supposed to be orthologous to the tomato *Lv* locus. Similarly, the *Ol-1*/*Ol-3* cluster on tomato chromosome 6 confers resistance to *Oidium lycopersicum* (*Oidium neolycopersici*), another powdery mildew of tomato. This cluster is flanked by markers TG025 and TG240, which are linked to CD025 and CT204 (Huang et al. 2000). The *Lt-6.1* QTL, linked to GC002, is also linked to CD025 and CT204 (Lefebvre et al. 1998), and is likely to correspond to the *Ol-1*/*Ol-3* loci tomato cluster. Colinearity of loci governing resistance to identical or similar pathogens was rarely described in the literature (Djian-Caporalino et al. 2001; Parrella et al. 2002; Thabuis et al. 2003). Functional orthology among resistance loci occurring in several species could be attributed to a common ancestral gene. Therefore, these genes could share similar mechanisms involved in plant-pathogen interaction.

Availability of molecular markers linked to QTLs controlling powdery mildew in pepper could facilitate marker-assisted selection in breeding programs aiming to transfer the resistance from H3 to elite breeding lines. Two of the above QTLs were mapped in pepper genomic regions where traits of interest were already located. The *Lt10.1* QTL mapped in the dominant gene cluster *Pvr4* – *Tsw* controlling respectively the resistance to potyviruses (PepMoV and PVY) and TSWV of pepper (Moury et al. 2000; Grube et al. 2000). The *Lt-6.1* QTL was located near the GC002 marker, corresponding to the gene coding the capsanthin-capsorubin synthase and responsible for the *y* locus controlling the red- vs. yellow-fruited pepper (Lefebvre et al. 1998). Because of distinct allelic origins, those linkages will cause difficulties in breeding elite

lines carrying resistance to *L. taurica* and PepMoV or TSWV, and in breeding resistant yellow-fruited varieties. Large segregating populations and marker-assisted screening will aid to select recombinant individuals having these traits in tandem order. Selection of such recombinants is crucial for the development of novel parental lines in breeding programs.

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Note added in proof QTLs for resistance to *Oidium lycopersici* from *Lycopersicon parviflorum* were recently reported by Bai et al. (2003). They show a colinear position with the *Lt-6.1* and *Lt-9.1* QTLs on pepper.