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Mapping of new resistance (*Vr2*, *Rm1*) and ornamental (*Di2*, *pl*) Mendelian trait loci in peach

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Abstract Peach powdery mildew is one of the major diseases of the peach. Various sources of resistance to PPM have thus been identified, including the single dominant locus *Vr2* carried by the peach rootstock 'Pamirskij 5'. To map *Vr2*, a linkage map based on microsatellite markers was constructed from the F_2 progeny (WP^2) derived from the cross 'Weeping Flower Peach' × 'Pamirskij 5'. Self-pollinations of the parents were also performed. Under greenhouse conditions, all progenies were scored after artificial inoculations in two classes of reactions to PPM (resistant/susceptible). In addition to *Vr2*, WP^2 segregated for three other traits from 'Weeping Flower Peach': *Rm1* for green peach aphid resistance, *Di2* for double-flower and *pl* for weeping-growth habit. With their genomic locations unknown or underdocumented, all were phenotyped as Mendelian characters and mapped: *Vr2* mapped at the top of LG8, at 3.3 cM, close to the CPSCT018 marker; *Rm1* mapped at the bottom of LG1, at a position of 116.5 cM, cosegregating with the UDAp-467 marker and in the same region as *Rm2* from 'Rubira'®; *Di2* mapped at 28.8 cM on LG6, close to the MA027a marker; and *pl* mapped at 44.1 cM on LG3 between the MA039a and SSRLG3_16m46 markers. Furthermore, this study revealed, for the first time, a pseudo-linkage between two traits of the peach: *Vr2* and the *Gr* locus, which controls the red/green color of foliage. The present work therefore constitutes a significant preliminary step for implementing marker-assisted selection for the four major traits targeted in this study.

Keywords Powdery mildew · Green peach aphid · Double-flower · Weeping-growth habit · SSR · Pseudo-linkage

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Introduction

Most modern peach cultivars are susceptible to peach powdery mildew (PPM), a major disease of the peach (*Prunus persica* L. Batsch). PPM is caused by *Podosphaera pannosa* var. *persicae* (Weinhold 1961; Monet 1983). The development of circular white spots on leaves shoots and fruits is characteristic of PPM attacks that result in unattractive fruit for the fresh market, leaf drop and shoot stunting. Numerous applications of fungicide are thus required throughout the entire season of peach production to fight this fungal disease (Saunier 1973). In this context, resistant cultivars to PPM appear as a desirable alternative for

effective control of the disease and as an environmentally safe solution.

Various studies were conducted to identify sources of resistance to PPM in peach and in species belonging to the same subgenus *Amygdalus* (Saunier 1973; Alexandri and Filip 1977; Angelov 1980; Paunovic et al. 1985; Rodriguez et al. 1990; Perez et al. 1993). Different factors of resistance to PPM were thus identified from wild species that are closely related to *P. persica*, such as *Prunus kansuensis* Rehder (Smykov et al. 1982) and *Prunus davidiana* (Carr.) French. Regarding *P. davidiana*, nine quantitative trait loci (QTL) for PPM resistance were detected in clone P1908, including two major QTLs (*qPM.SP-G6*, *qPM.SP-G8*) located in linkage groups (LGs) 6 and 8 (Dirlewanger et al. 1996; Foulongne et al. 2003a). More recently, a Mendelian trait locus for PPM resistance, *Vr3*, derived from almond (*Prunus dulcis* (Miller) Webb), was mapped to the upper region of LG2 of two genetic maps constructed from two interspecific populations derived from the initial peach × almond cross 'Texas' × 'Earlygold' (Donoso et al. 2016). In *Prunus* but in a different subgenus (*Prunophora*), one main QTL for resistance to PPM was identified in the same linkage group as *Vr3* (LG2) in the apricot (*Prunus armeniaca* L.) cultivar 'Goldrich' as well as another one with lower effects in LG3 (Salazar et al. 2016), using an F_1 mapping population ('Goldrich' × 'Currot'). Minor QTLs were also detected in LG4 and LG8 of the susceptible parent 'Currot' as well as another QTL in LG5 of 'Bergeron', using a different progeny ('Bergeron' × 'Currot'). However the QTLs were not stable over the years and their significance levels and effects were highly dependent on the year-to-year variations of the environmental conditions, demonstrating a polygenic nature and quantitative inheritance of PPM resistance in apricot.

In peaches, cultivars without foliar glands (*ee*) are considered very susceptible to PPM compared to those with nectaries. Accordingly, all commercial cultivars have reniform (*EE*) or circular (*Ee*) nectaries because peach breeders routinely eliminate eglandular seedlings (Monet 1983). Among the cultivars that exhibit foliar glands, high resistance to PPM, which is conferred by several QTLs (Pacheco et al. 2009), was identified in the canning peach cultivar 'Oro' (Rodriguez and Sherman 1990). Conversely, a single dominant locus of resistance to PPM was described in the peach cultivars 'Ferganskij Zheltyj' (Dabov 1974, 1975) and 'Ustoichivy Pozdni' (Perfilyeva 1982; Tsukanova et al. 1980, 1982; Smykov et al. 1982; Iliev 1985), both derived from *Prunus ferganensis* (Kost. and Riab.), which is considered a wild undomesticated peach (Verde et al. 2013). Subsequently, Dabov (1983) demonstrated that two single loci determined the level of resistance to PPM: a locus controlling high resistance (*Vr*) and the other, controlling both medium and low resistance (*Sf*). The dominant allele of *Vr* was found to be epistatic to *Sf*. For *Sf*, the allele for medium resistance is dominant over the allele for low resistance; the latter is typical of eglandular cultivars such as the canning peach cultivar 'Paloro' (Dabov 1975). In support of this finding, two QTLs for resistance to PPM were detected from *P. ferganensis*: *qPM.PF-G7* tightly linked to the *E* locus on LG7 (Quarta et al. 1998, 2000; Verde et al. 2002) and *qPM.PF-G8* on the top of LG8, which was detected only one year (Verde et al. 2002). Unfortunately, neither of these two QTLs were confirmed, either on LG7 (Dettori et al. 2001; Verde et al. 2004) or LG8 (Verde et al. 2005).

More recently, another single dominant locus of resistance to PPM (*Vr2*) was identified in the peach rootstock cultivar 'Pamirskij 5' (Pascal et al. 2010) using several progenies derived from crosses between the red-leaf cultivar 'Rubira'® and 'Pamirskij 5', among which an F_2 mapping progeny, PR^2 (Lambert and Pascal 2011). In these progenies, a strong linkage was demonstrated between *Vr2* and the *Gr* locus (Pascal et al. 2010), which controls the red/green (*Gr*/*gr*) color of leaves (Blake 1937). However, as *Gr* was mapped near the breakpoint of the region corresponding to a reciprocal translocation between LG6 and LG8 (Jáuregui et al. 2001; Yamamoto et al. 2001; Lambert and Pascal 2011), it was not possible to unambiguously map *Vr2* in the PR^2 map (unpublished data). As a result the position of *Vr2* remained unclear.

Hence, the first objective of our study was to map the single dominant locus *Vr2*, which controls the resistance to PPM conferred by 'Pamirskij 5'. To this end, we built a linkage map based on simple sequence repeat (SSR) markers from an F_2 progeny derived from the cross 'Weeping Flower Peach' × 'Pamirskij 5', called WP^2. 'Weeping Flower Peach' was first chosen for its susceptibility to PPM, and its green foliage allowing us to avoid the issue caused by the translocation associated with the red foliage, as in PR^2.

Additionally, 'Weeping Flower Peach' was known to carry other Mendelian traits of interest, such as *Rm1*, for green peach aphid resistance (GPA) (Massonié et al. 1982), *Di2* for double-flower and *pl* for weeping-growth habit (Monet et al. 1988). Each of these single traits from 'Weeping Flower Peach' had been previously used in a peach breeding program (Monet 1983), particularly to develop GPA-resistant or ornamental peach varieties. However, the genomic locations of *Rm1* (Monet and Massonié 1994) and *Di2* (Lammerts 1945; Beckman et al. 2012) were unknown, and that one of *pl* was underdocumented (Dirlewanger and Bodo 1994; Chaparro et al. 1994; Hollender et al. 2013). Therefore, in addition to the first objective (*Vr2*), this study aimed to identify the genomic regions involved in these characters (*Rm1*, *Di2*, *pl*) and to obtain preliminary results that could be useful for developing markers highly associated with these traits, in order to implement marker-assisted selection (MAS) for the four major traits in peach breeding programs.

Materials and methods

Plant materials

Four different progenies were developed in this study (Table 1), three of which (S_{1a}, S_{1b}, F_1) were used to check the Mendelian determinism of the four traits examined, as well as their status in the parents (homozygous/heterozygous), and the last one for mapping the characters targeted above. The first progeny (S_{1a}) was derived from the selfing of 'Pamirskij 5' (clone S6146), a green leaf peach rootstock known for its resistance to PPM determined by a single dominant locus called *Vr2* (Pascal et al. 2010). The second (S_{1b}) was derived from the selfing of 'Weeping Flower Peach' (clone S2678), an ornamental green leaf peach variety of unknown origin, introduced in France in the 1960s from Clemson University (South Carolina—USA). S2678 was studied for its resistance to GPA determined by a single dominant trait called *Rm1* (Monet and Massonié 1994). The double-flower trait is also controlled by a single dominant trait called *Di2* (Beckman et al. 2012) and the weeping-growth habit trait is conferred by a single recessive trait called *pl* (Monet et al. 1988; Dirlewanger and Bodo 1994). The third progeny was an F_1 derived from a controlled cross between the two above mentioned cultivars. The last progeny, referred to as WP^2, was an F_2 progeny of 89 seedlings obtained from the selfing of a single individual of the F_1 progeny.

Phenotypic traits evaluation

S_{1ab}, F_1 and F_2 progenies were observed for their reactions to PPM and to GPA under greenhouse conditions, according to the same methods as those used in previous studies, i.e., after artificial inoculation by *P. pannosa* (Pascal et al. 2010) and artificial infestation by *Myzus persicae* (Pascal et al. 2002; Lambert and Pascal 2011). Both traits were scored as Mendelian characters, as there were clear differences between the two classes of phenotypes, i.e., resistant to PPM (no visible symptoms or a few small and rare white spots on the whole plant)/susceptible (large white spots on numerous leaves and young stems with an abundant sporulation); resistant to GPA (non-colonization by aphid—non-leaf curling—presence of reddish spots)/susceptible (colonization by aphid—leaf curling—absence of reddish spots). The type of foliar gland (reniform/circular) was not recorded since each of the parents (S6146, S2678) exhibited reniform foliar glands (*EE*). As a result, WP^2 did not segregate for this trait. Under orchard conditions, each of the progenies was then evaluated for double-flower and weeping-growth habit traits as Mendelian characters, i.e., double/single flower (Monet et al. 1988; Beckman et al. 2012) and weeping/standard growth habit (Monet et al. 1988; Dirlewanger and Bodo 1994; Chaparro et al. 1994).

DNA isolation and marker analysis

Samples of young leaves from the seedlings and from the two parents of the WP^2 were collected in spring and stored at −80 °C until DNA extraction. Genomic DNA was subsequently isolated using the Qiagen DNeasy 96 Kit (Qiagen, Valencia, CA, USA) according to the manufacturer's instructions. DNA concentration was measured using a Thermo Fisher Scientific NanoDrop™ spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA) and further assessed by electrophoresis on a 1.0% agarose gel. The *Prunus* SSR primer pairs used in this study were the same as those previously mapped in the report by Lambert and

Table 1 Segregation ratios observed in S_{1ab} (selfs), F_1 and F_2 progenies for reactions to peach powdery mildew (*Vr2*) and to green peach aphid (*Rm1*), and for double-flower (*Di2*) and weeping-growth habit (*pl*) traits

Cross	Observed ratio (expected)				*P* value
	Powdery mildew (*Vr2*)		Expected ratio	χ^{2*} (1 df)	
	Resistant	Susceptible			
(Pamirskij 5)^2 S_{1a}	131	0	1:0	–	–
(Weeping Flower Peach)^2 S_{1b}	0	25	0:1	–	–
Weeping Flower Peach × Pamirskij 5 F_1	59	0	1:0	–	–
[(Weeping Flower Peach × Pamirskij 5)3]^2 F_2	65 (66.75)	24 (22.25)	3:1	0.1835	0.6684
Cross	Observed ratio (expected)				*P* value
	Green peach aphid (*Rm1*)		Expected ratio	χ^{2*} (1 df)	
	Resistant	Susceptible			
(Pamirskij 5)^2 S_{1a}	0	131	0:1	–	–
(Weeping Flower Peach)^2 S_{1b}	55	0	1:0	–	–
Weeping Flower Peach × Pamirskij 5 F_1	59	0	1:0	–	–
[(Weeping Flower Peach × Pamirskij 5)3]^2 F_2	70 (66.75)	19 (22.25)	3:1	0.633	0.4263
Cross	Observed ratio (expected)				*P* value
	Flower type (*Di2*)		Expected ratio	χ^{2*} (1 df)	
	Double	Single			
(Pamirskij 5)^2 S_{1a}	0	131	0:1	–	–
(Weeping Flower Peach)^2 S_{1b}	35 (32.25)	8 (13.75)	3:1	0.938	0.3328
Weeping Flower Peach × Pamirskij 5 F_1	31 (29.5)	28 (29.5)	1:1	0.152	0.6961
[(Weeping Flower Peach × Pamirskij 5)3]^2 F_2	54 (63)	30 (21)	3:1	5.142	0.0323
Cross	Observed ratio (expected)				*P* value
	Weeping-growth habit (*pl*)		Expected ratio	χ^{2*} (1 df)	
	Weeping	Standard			
(Pamirskij 5)^2 S_{1a}	0	131	0:1	–	–
(Weeping Flower Peach)^2 S_{1b}	43	0	1:0	–	–
Weeping Flower Peach × Pamirskij 5 F_1	0	59	0:1	–	–
[(Weeping Flower Peach × Pamirskij 5)3]^2 F_2	36 (22.25)	53 (66.75)	1:3	11.329	0.00076

* Chi square test was used for the given probabilities

Pascal (2011). Four SSRs, AMPPG125, AMPPG123, AMPPG127 and AMPPG131 (Shen et al. 2013), and SSRLG3_16m46 (S. Decroocq personal communication) were added to complete two of the linkage groups. For the latter, the following primer pair was used: forward primer, CGCGCTCTTTATGATTC TTC and reverse primer, GATTTTGCTTGCTTGGA CGT. The SSRs were initially screened for the two parents and six individuals of the progeny. Subsequently, the polymorphic SSRs were used to map the entire WP^2 progeny. The SSRs were amplified using FAM, HEX, NED or ATTO565 dye-labeled forward primers and standard reverse primers. PCR was performed in a total volume of 15 µl using the GoTaq G2 Flexi DNA polymerase Kit (Promega, Madison, WI, USA) and included the following components: 15 ng of template DNA, 1× buffer, 1.5 mM of $MgCl_2$, 0.2 mM of dNTPs, 0.25 units of

GoTaq polymerase and 0.2 μM of each primer. PCR was performed on a Mastercycler®ep gradient thermal cycler (Eppendorf GmbH Instrumente, Hamburg, Germany) using a program of 15 min at 95 °C, followed by 35 cycles at 95 °C for 30 s, 55 °C for 45 s, and 72 °C for 30 s, with a final extension at 72 °C for 8 min. PCR products were mixed and diluted 90–200 times depending on the signal intensity and subsequently loaded onto an Applied ABI 3730 sequencer (Applied Biosystems, Foster City, CA, USA) using Genescan 500 LIZ (Life Technologies SAS) as a size standard and GeneMapper 4.0 software.

Linkage map construction and mapping of *Vr2, Rm1*, *Di2* and *pl*

Segregation data for the four single traits observed in the mapping progeny WP^2 were included in the SSR dataset as dominant (*Vr2*, *Rm1*, *Di2*) or recessive (*pl*) markers. Deviations from Mendelian ratios were tested using a Chi square goodness-of-fit test ($P < 0.05$) on segregation data. Linkage analysis was performed with Mapmaker/EXP 3.0 software (Lincoln et al. 1992). Linkage groups were established using an initial logarithm of the odds (LOD) threshold of >3.0 and a recombination fraction of 0.40. Marker distances were calculated using the Kosambi mapping function (Kosambi 1944). The "error detection" option was used and possible errors were checked and corrected when necessary. Map figures were drawn using MapChart 2.3 software (Voorrips 2002).

Results

Segregation analyses

For all traits examined in this study (Table 1), the S_{1ab} and F_1 progenies segregated according to the expected ratios (0:1, 3:1, 1:1), indicating a monogenic determinism either dominant (*Vr2*, *Rm1*, *Di2*) or recessive (*pl*). Segregation data in the F_2 progeny confirmed this determinism, particularly for *Vr2* and *Rm1*, even though distorted segregations were observed for both *Di2* and *pl* ($\chi^2 = 5.142$ and 11.329, respectively) when compared to the expected ratios, with an excess of trees exhibiting the recessive phenotype. Based on the observed segregations (Table 1), the genotypes of both parents (S6146, S2678) for the four studied traits are summarized in Table 2. 'Pamirskij 5' is homozygous for the four studied traits, while 'Weeping Flower Peach' is homozygous for *Vr2*, *Rm1* and *pl* and heterozygous for *Di2*.

WP^2 linkage map construction

Of the initial 121 SSR markers screened, 56 were identified as polymorphic and used to construct the WP^2 map. The 56 SSR loci and the 4 phenotypic traits (*Vr2*, *Rm1*, *Di2* and *pl*) were mapped with an LOD score of 5.0 at 58 map positions on eight linkage groups, as expected in the peach. The resulting map (Fig. 1) covered a total genetic distance of 563.7 cM for an average distance of 9.7 cM between map positions (Table 3). Five gaps larger than 25 cM were observed in five of the linkage groups (LG1, LG2, LG4, LG5 and LG7). The physical distance covered by the entire map corresponded to 74.6% of the Peach genome sequence v2.0 (Table 3), with the lowest coverage (64.65%) for LG3 and the highest coverage (83.47%) for LG1. The distribution and positions of the markers over the linkage groups were consistent with their known positions in the Peach genome sequence v2.0, except for two physically close SSRs (MA023a and EPPCU5628), which cosegregated at the same map position, reflecting a lack of recombination in the mapped individuals. Significant deviations from the Chi square expectations were observed for 11 markers mapped on three linkage groups (Fig. 1), of which, two linkage groups (LG3 and LG6) included Mendelian traits *pl* and *Di2*, respectively. LG3 deviations reflected a lack of homozygous individuals for the alleles from 'Pamirskij 5' and an excess of homozygous individuals for 'Weeping Flower Peach'. Opposing results were observed for LG6, and all markers except for EPPCU2957 were heavily distorted ($P < 0.001$ to $P < 0.0001$). No translocation event was observed between LG6 and LG8.

Mapping of *Rm1, pl, Di2* and *Vr2*

The four targeted traits mapped unambiguously to single positions in four different linkage groups (Fig. 1): *Rm1* co-segregated with UDAp-467 at a position of 116.8 cM, at the bottom of LG1; *pl* mapped to a position of 44.1 cM on LG3; *Di2* mapped to a position of 28.8 cM on LG6; and *Vr2* mapped near the

Table 2 Genotypes of the parents for allelic pairs *Vr2*/*vr2*, *Rm1*/*rm1* or *Rm2*/*rm2*, *Di2*/*di2* and *pl*/*Pl* deduced from the segregation analysis

Parents (peach cultivars)	Resistance to peach powdery mildew (*Vr2*)	Resistance to green peach aphid (*Rm1*)	Double-flower trait (*Di2*)	Weeping-growth habit trait (*pl*)
Pamirskij 5 (S6146)	*Vr2Vr2*	*rm1rm1*	*di2di2*	*PlPl*
Weeping Flower Peach (S2678)	*vr2vr2*	*Rm1Rm1*	*Di2di2*	*plpl*

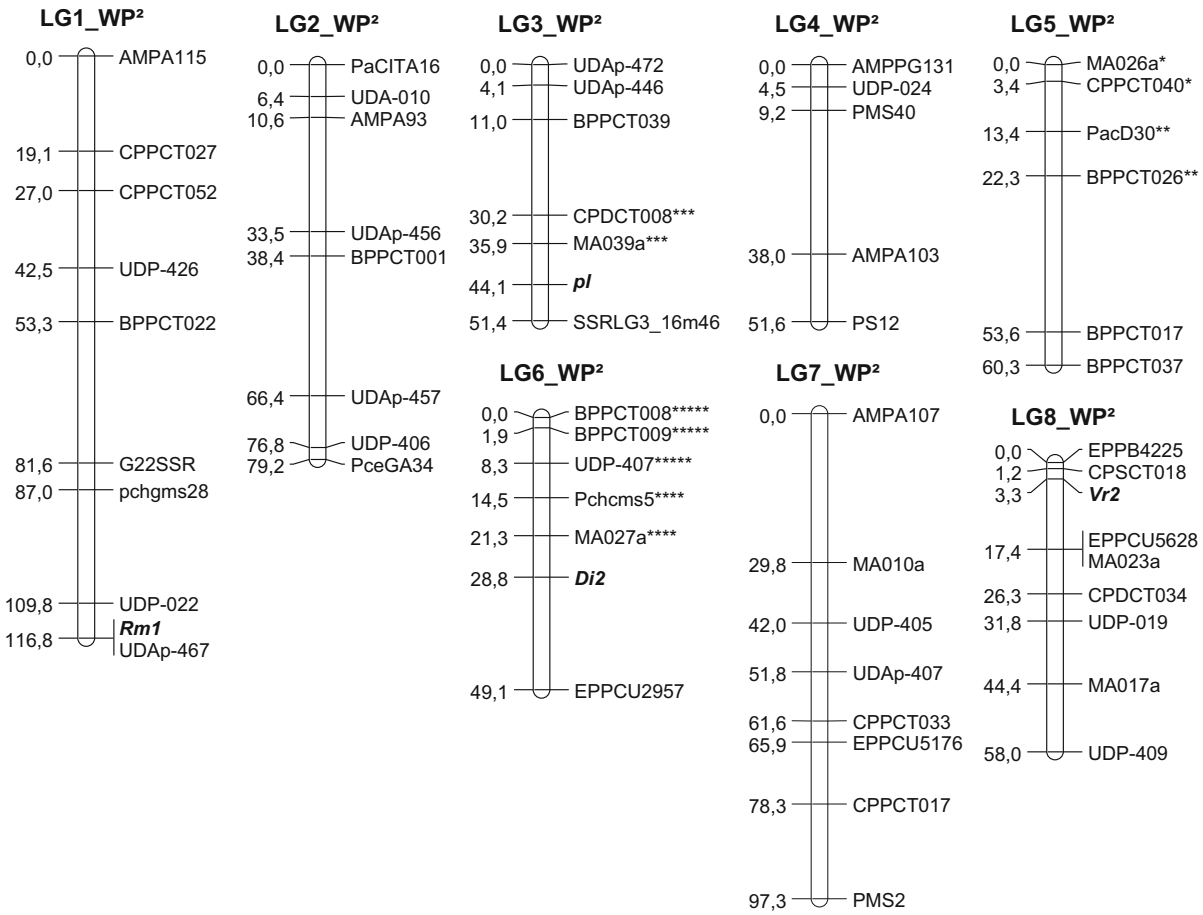

Fig. 1 Linkage map derived from the 'Weeping Flower Peach' × 'Pamirskij 5' F_2 progeny. The four Mendelian traits are indicated in *bold* and *italics*. SSR loci with *asterisks* after the locus name exhibit distorted segregation (*$P < 0.02$, **$P < 0.01$, ***$P < 0.005$, ****$P < 0.001$ and *****$P < 0.0001$)

upper end of LG8, at 3.3 cM, close to the CPSCT018 marker. The regions including each of the traits spanned genetic distances comprised between 7.2 cM (*Rm1*) and 27.8 cM (*Di2*) which correspond to physical distances comprised between 2,880,352 bp (*Rm1*) and 7,317,354 bp (*Di2*) in the Peach genome v2.0 pseudomolecules (Table 4).

Discussion

Segregation analyses

As expected (Monet et al. 1988; Monet and Massonié 1994; Beckman et al. 2012; Pascal et al. 2010), all segregations observed in the S_{1ab}, F_1 and F_2 progenies

Table 3 WP^2 map description and coverage compared to the Peach v2.0 pseudomolecules/scaffolds

Linkage group	Boundary markers	Interval (bp) between markers	Scaffold length (bp)[a,b]	% Scaffold length covered	Genetic distance	# of map positions	Avg genetic distance between map positions[c]
LG1	AMPA115/ UDAp-467	39,940,763	47,851,208	83.47	116.8	9	13
LG2	PaCITA16/ PceGA34	23,287,713	30,405,870	76.59	79.2	8	9.9
LG3	UDAp-472/ SSRLG3_16m46	17,692,607	27,368,013	64.65	51.4	7	7.3
LG4	AMPPG131/PS12	19,786,557	25,843,236	76.57	51.6	5	10.3
LG5	MA026a/ BPPCT037	12,161,396	18,496,696	65.75	60.3	6	10
LG6	BPPCT008/ EPPCU2957	20,082,011	30,767,194	65.28	49.1	7	7
LG7	AMPA107/PS2	17,009,643	22,388,614	75.97	97.3	8	12.2
LG8	EPPB4225/UDP-409	18,406,332	22,573,980	81.54	58	8	7.3
Total		168,367,022	225,694,811	74.60	563.7	58	9.7

[a] Scaffold information is available at GDR: http://www.rosacea.org/peach/genome

[b] The eight Peach v2.0 scaffolds (Pp01 to Pp08) correspond to the eight linkage groups (LG1 to LG8)

[c] Average genetic distance between map positions of markers

Table 4 Positions of the four Mendelian traits and comparison with the Peach v2.0 pseudomolecules

Linkage Group	Mendelian trait	Map position	Boundary markers	Position in the Peach v2.0 pseudomolecules (bp)[a,b]	Interval between markers (bp)	Interval between markers (cM)
LG1	*Rm1*	116.8	UDP-022	43,622,191–315	2,880,352	7.2
			UDAp-467	46,502,361–543		
LG3	*pl*	44.1	MA039a	17,772,071–090	4,039,802	15.5
			SSR-LG3-16m46	21,811,784–873		
LG6	*Di2*	28.8	MA027a	22,759,522–666	7,317,354	27.8
			EPPCU2957	30,376,733–876		
LG8	*Vr2*	3.3	CPSCT018	123,784–NA	3,769,479	16.2
			EPPCU5628	3,893,065–263		

[a] Marker positions are those of the first bases of the forward and the reverse primers used to amplify the SSR markers by PCR as reported in the GDR: http://www.rosacea.org/peach/genome

[b] The four linkage groups (LG1 to LG8) correspond to the Peach v2.0 pseudomolecules (Pp01 to Pp08) respectively

complied with a dominant (*Vr2*, *Rm1*, *Di2*) or recessive (*pl*) determinism of monogenic traits. As indicated in the linkage map, distorted segregations were observed in three linkage groups of the WP^2 map, of which, two (LG3 and LG6) included Mendelian traits (*Di2* and *pl*). Distorted segregations are common events and are more frequently observed in inter-specific crosses (Joobeur et al. 1998; Jáuregui et al. 2001; Foulongne et al. 2003b); they could be due to local preferential allelic combinations linked to the different origin of the parents. In LG6, distorted segregations were due to a lack of individuals

homozygous for 'Weeping Flower Peach' alleles in the upper region of the group. More specifically, for the *Di2* trait, Beckman et al. (2012) reported similar distortions of this trait in F_2 progenies of small size derived from 'Red Weeping' clone PI091459. A distorted segregation, albeit less pronounced, was also observed for one F_2 progeny in the report by Monet et al. (1988) regarding the *pl* trait.

Peach powdery mildew resistance trait (*Vr2*)

In this study, we mapped for the first time the first single dominant locus of resistance to PPM (*Vr2*) in peach. *Vr2* has been assigned to the upper region of LG8 at position 3.3 cM in the WP^2 map, close to the CPSCT018 marker. This result answers the question raised by Arús et al. (2012) regarding the location of *Vr2* that these authors initially placed on LG6 of 'Pamirskij 5' instead of LG8, following Pascal et al. (2010). The former location of *Vr2* on LG6 was initially consistent with the position of the major QTL for resistance, *qPM.SP-G6*, detected on LG6 of *P. davidiana* P1908 (Foulongne et al. 2003a). Nevertheless, the position of *Vr2* on LG8 could not be ignored given that the genetic linkage observed between *Vr2* and *Gr* on LG6 (Pascal et al. 2010) could have been due to the reciprocal translocation identified between LG6 and LG8 in different genetic maps (Jáuregui et al. 2001; Yamamoto et al. 2001; Lambert and Pascal 2011). The present mapping of *Vr2* clarifies this point and constitutes a starting point for the fine mapping of the region of LG8 including *Vr2*. From a peach breeder point-of-view, the mapping of *Vr2* brings strong opportunities for implementing MAS for resistance to PPM in peach.

Interestingly, the region including *Vr2* in 'Pamirskij 5' is close to the region containing the QTL *qPM.PF-G8*, which was previously mapped on the P × F map constructed from a BC_1 progeny derived from *P. ferganensis* (Verde et al. 2002). *qPM.PF-G8* was detected in a region of 3 cM on the top of LG8, close to FG229 and FG73a markers. However, neither this QTL was confirmed in further studies using the same BC_1 progeny, nor the other major QTL, *qPM.PF-G7*, which is tightly associated with the *E* locus on LG7 (Quarta et al. 1998, 2000; Verde et al. 2002, 2004). PPM evaluations were performed under orchard conditions through natural infection (consequently not homogenous over the 4 years of the trial), which could explain that they were not confirmed afterwards (Dettori et al. 2001; Verde et al. 2005). The small size of the progeny (77 trees) used may also explain the low efficiency of the QTL detection. Likewise, these two resistance factors to PPM (*qPM.PF-G7*, *qPM.PF-G8*) were detected as quantitative traits whereas monogenic trait loci were expected, according to Dabov (1974, 1975, 1983) when using *P. ferganensis*. In addition, Verde et al. (2002) observed eglandular peach seedlings resistant to PPM, which means that the region including the QTL *qPM.PF-G7* associated with the *E* locus and the region containing the QTL *qPM.PF-G8* independently affect the resistance. However, the absence of accurate data does not allow for a conclusion to be drawn. Nevertheless, these results are consistent with the hypothesis proposed by Dabov (1983), who indicated that two loci, *Vr* and *Sf*, were responsible for the resistance to PPM from *P. ferganensis*, *Vr* being epistatic to *Sf*. Therefore, complementary studies would be appropriate to determine the quantitative nature and location of *qPM.PF-G8* on LG8 and *qPM.PF-G7* on LG7 comparatively to *Vr* and *Sf*, as well as their possible epistatic relationship.

Our results from WP^2 clearly demonstrate the implication of the *Vr2* locus as a major factor of resistance to PPM. Unfortunately, and in contrast to the BC_1 progeny (Verde et al. 2002), there was no glandular/eglandular segregation in WP^2 due to the homozygosity (*EE*) of both parents for the *E* trait. As *Vr2* from 'Pamirskij 5' and *qPM.PF-G8* from *P. ferganensis* are both located in the same upper region of LG8, further investigations are needed to determine whether only one or two distinct factors of resistance to PPM are included in this genomic region. This is all the more important since the origin of 'Pamirskij 5' remains unknown, as well as its genetic relationship with *P. ferganensis*.

A major QTL for resistance to PPM (*qPM.SP-G8*) was also detected in LG8 from the wild species *P. davidiana*. However, *qPM.SP-G8* is relatively far from *Vr2*, spanning between 17.28 and 19.8 cM (Dirlewanger et al. 1996; Foulongne et al. 2003a). As a result, at least two different genomic regions may be involved in resistance to PPM in the upper part of LG8 and potentially useful in breeding programs.

From the results reported in the available studies, PPM resistance seems to be often quantitative and polygenic in *Prunus* species. In sweet cherry (*P. avium*

L.), two close QTLs for resistance to PPM were detected at the bottom of LG1 of the cultivar PMR-1 (Oraguzie et al. 2012) although Olmstead et al. (2001) originally suggested a single-gene inheritance of the PPM resistance using several progenies derived from the same cultivar PMR-1. More recently (Salazar et al. 2016), several QTLs for resistance to PPM were reported in apricot (*Prunus armeniaca* L.) among which one main QTL in LG2 of the cultivar 'Goldrich' as well as another one with lower effects in LG3. However, the QTL in LG2 was not in the same region as the *Vr3* gene from almond (Donoso et al. 2016) when comparing the positions of their respective flanking markers. From the same study (Salazar et al. 2016), minor QTLs were also detected in LG4, LG5 and LG8 of the susceptible cultivar 'Currot'; nevertheless, they were not stable over the years, suggesting strong influence of the environmental conditions. None of the resistance factors identified in other *Prunus* species were common to those described in *P. persica* and close species such as *P. davidiana*. Moreover, the fact that resistance to PPM was often quantitative and polygenic in most of the *Prunus* species studied so far, adds even more interest for the use of Mendelian trait loci such as *Vr2* in peach breeding programs for PPM resistance. At the peach genome scale and in addition to *Vr2* and *qPM.SP-G8*, it would be therefore appropriate to take into account the other Mendelian traits and QTLs for resistance previously reported from species genetically compatible and easy to cross with peach and to consider their use in peach breeding programs aimed at resistance to PPM, i.e., *Vr3* on LG2 (Donoso et al. 2016), *qPM.SP-G6* on LG6 (Foulongne et al. 2003a) and *qPM.PF-G7* on LG7 (Verde et al. 2002) from *P. dulcis*, *P. davidiana* and *P. ferganensis*, respectively. All these various factors of resistance represent a highly valuable resource for implementing breeding programs for durable resistance to PPM in peach.

This work also demonstrates that the genetic linkage previously identified between *Vr2* and *Gr* in several progenies derived from 'Rubira'® (Pascal et al. 2010) was, in fact, a pseudo-linkage due to the reciprocal translocation detected in the PR^2 map (Lambert and Pascal 2011). Indeed, one of the consequences of a reciprocal translocation between two non-homologous chromosomes, a so-called heterozygote, is suppression during the metaphase of genetic recombination close to the translocation breakpoints. This suppression of recombination affects linkage relationships, resulting in a pseudo-linkage between genes and/or traits located near the translocation breakpoint. These genes behave as if they were linked, although these traits originated on non-homologous regions (Farré et al. 2011). Another consequence of this suppression is the generation of disturbed linkage maps (Farré et al. 2012), as recorded by Lambert and Pascal (2011). A pseudo-linkage can be easily detected because it results in unexpected linkages between morphological and/or molecular markers that are independent in other crosses. This was the case for *Vr2* and *Gr*, as well as for the SSRs belonging to the translocated regions of LG6 and LG8 of PR^2 (Lambert and Pascal 2011). The mapping of *Vr2* from the WP^2 allowed for this issue to be solved and clearly assigned *Vr2* to LG8. This constitutes the first case of a pseudo-linkage observed between two Mendelian traits in peach.

Green peach aphid resistance trait (*Rm1*)

Regarding the resistance to GPA, one of the main pests of the peach, *Rm1*, was mapped to the bottom of LG1 at a position of 116.8 cM, cosegregating with the UDAp-467 marker in the WP^2 map (Fig. 1). *Rm1* is the second Mendelian locus of resistance to GPA mapped in peach. Its location corresponds to that of *Rm2*, which was previously mapped to the same genomic region of LG1 in the PR^2 map, spanning a 2.5 cM interval between pchgms29 and UDAp-467 markers (Lambert and Pascal 2011). This result partly answers the question as to whether one or several regions are involved in the resistance to GPA conferred by these two peach accessions. Indeed, each of them confers a strong antixenosis-type resistance that prevents plant colonization by aphids (Monet and Massonié 1994; Kfoury and Massonié 1995; Sauge et al. 1998a, 2002; Pascal et al. 2002). However, clear differences in aphid behavior have been reported between *Rm1* and *Rm2* (Sauge et al. 1998b, 2006), suggesting that the underlying resistance mechanisms may differ. The present study shows that *Rm1* and *Rm2* are controlled by only one relatively narrow region of the peach genome. Further studies are needed to reach a definitive conclusion on the involvement of one or two distinct loci in the GPA resistance conferred by S2678 and S2605. Nevertheless, the information provided in the present study should enable us to

focus our future efforts on this single genomic region located at the bottom of LG1, in order to identify these two potentially distinct loci of resistance to GPA.

Double-flower (*Di2*) and weeping-growth habit (*pl*) traits

Two distinct loci control the double-flower trait in peach. The first was described by Lammerts (1945) as a single-gene recessive trait (*Di*/*di*). The recessive locus d_i was later found to be linked to the pillar locus (*pi*; also known as *br* for broomy or *co* for columnar) and was initially mapped to LG1 (Chaparro et al. 1994; Rajapakse et al. 1994; Sosinski et al. 2000). By comparative mapping, *di* was then assigned to LG2 of the *Prunus* reference map (Joobeur et al. 1998; Dirlewanger et al. 2004; Arús et al. 2012). The second double-flower trait was reported by Beckman et al. (2012) as a single-gene dominant trait (*Di2*/*di2*). However, the location of *Di2*, derived from 'Red Weeping', in the peach genome remained unknown until today. In our study, the double-flower locus derived from S2678 was mapped at 28.8 cM in the central part of LG6. Considering its dominant determinism and until further information regarding its location in 'Red Weeping', we suggest assimilating it to *Di2*.

Continuing the work initiated by Monet et al. (1988) regarding S2678, the weeping-growth habit trait is determined by a single recessive locus called *pl* (for 'pleureur' in French). Thereafter, the *pl* locus was mapped to the largest linkage group of a linkage map based on random amplified polymorphism DNA (RAPD) markers (Dirlewanger and Bodo 1994). The RAPD-based map included 8 linkage groups. Likewise, but from a different parent than S2678, the recessive *pl* (also called *we*) locus was mapped to one of the four linkage groups identified by Chaparro et al. (1994) and was linked to *PS2* (pollen-sterility) and *W* (white flower) loci. However, it was not possible to assign these groups to the current peach linkage groups due to the low transferability of isozymes (Chaparro et al. 1994) and RAPD (Dirlewanger and Bodo 1994) markers to other maps and, in particular, to the 'T × E' reference map for *Prunus*. In our study, *pl* from S2678 was mapped at 44.1 cM on LG3 of the WP^2 map. This is consistent with the preliminary studies of Hollender et al. (2013), which localized *pl* in a similar region of 2 Mb on LG3.

Taken together, our results revive interest for new studies on *Di2* and *pl* loci in the peach.

Conclusion

In the present study, two major traits for resistance to PPM and GPA and two ornamental characters (double-flower and weeping-growth habit) were mapped in peach; these included *Vr2* (LG8) from 'Pamirskij 5' and *Rm1* (LG1), *Di2* (LG6) and *pl* (LG3) from 'Weeping Flower Peach'. This preliminary step represents a good starting point to allow the implementation of MAS for these four traits of interest. However, further work on the development and routine use of molecular markers associated with these traits in peach breeding programs remains to be done. In addition to previous genetic and mapping studies conducted in the peach and closely related species, the mapping of *Vr2* and *Rm1* should be most useful for developing durable resistance against these two major bio-aggressors, in particular when combined with major QTLs. Mapping information on *Di2* and *pl* should also make it possible to develop new ornamental peach cultivars for gardens and parks. Furthermore, this study revealed, for the first time in peach, a pseudo-linkage between two major traits (*Vr2* and *Gr*). More broadly, the results presented here should contribute to the understanding of underlying genes governing the resistance to PPM and GPA, floral patterning regulation and tree architecture in peach.

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