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Co-localisation of host plant resistance QTLs affecting the performance and feeding behaviour of the aphid *Myzus persicae* in the peach tree

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QTLs of aphid feeding behaviour on resistant hosts

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Abstract

The architecture and action of quantitative trait loci (QTLs) contributing to plant resistance mechanisms against aphids, the largest group of phloem-feeding insects, are not well understood. Comparative mapping of several components of resistance to the green peach aphid (*Myzus persicae*) was undertaken in *Prunus davidiana*, a wild species related to peach. An interspecific F_1 population of *Prunus persica* var. Summergrand × *P. davidiana* clone P1908 was scored for resistance (aphid colony development and foliar damage) and 17 aphid feeding behaviour (AFB) traits monitored by means of the electrical penetration graph technique. Seven resistance QTLs were detected, individually explaining 6.1 to 43.1% of the phenotypic variation. Consistency was shown over several trials. Nine QTLs affecting AFB were identified. All resistance QTLs except one co-located with QTLs underlying AFB. A *P. davidiana* resistance allele at the major QTL was associated with drastic reductions in phloem sap ingestion by aphids, suggesting a phloem-based resistance mechanism. Resistance was also positively correlated with aphid salivation into sieve elements, suggesting an insect response to restore the appropriate conditions for ingestion after phloem occlusion. No significant QTL was found for traits characterising aphid mouthpart activity in plant tissues other than phloem vessels. Two QTLs with effects on AFB but without effect on resistance were identified. SSR markers linked to the main QTLs involved in resistance are of potential use in marker-assisted selection for aphid resistance. Linking our results with the recent sequencing of the peach genome may help clarify the physiological resistance mechanisms.

Key words: quantitative trait loci (QTL); host plant resistance; aphid feeding behaviour; electrical penetration graph (EPG); comparative genetic mapping; SSR markers

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Introduction

Aphids, the largest group of phloem-feeding herbivores, cause significant losses in agriculture. These pests are a primary topic in studies about plant responses to biotic stresses. In many crop species, aphid resistance is governed by single, dominant genes of major effect (reviewed in Dogimont *et al.,* 2010). The resistance conferred by these genes is often specific to insect biotype, and its lifetime is limited due to the rapid development of virulence in insect populations. Thus, this type of resistance is not 'durable'. By contrast, polygenic resistance, conveying varying resistance, is assumed to be harder to overcome than monogenic resistance. The first experimental evidence for this was recently reported for a plant-virus interaction (Palloix *et al.*, 2009). A guiding assumption regarding durability is that the more resistance factors there are to break down, the more genomic mutations will be required for the pathogen to become virulent; thus, virulence is less probable. Because quantitative resistance is controlled by multiple loci, referred to as quantitative trait loci (QTLs), and does not comply with simple Mendelian inheritance, selecting for these QTLs is difficult. To facilitate their introgression into cultivated germplasm, numerous QTL analyses have been undertaken (Yencho *et al*., 2000). Resistance QTLs have been analysed in relation to several physical and biochemical plant traits that likely correspond to distinct mechanisms, such as leaf pubescence and constitutive concentration or enzymatic activity of repulsive or toxic compounds (Maliepaard *et al*., 1995; Lee *et al*., 1998; Kliebenstein *et al*., 2002; Schranz *et al*., 2009). Several studies have also been devoted to mapping QTLs for resistance to aphids, mostly on annual crops (reviewed in Dogimont *et al.,* 2010). Some of these have endeavoured to clarify the function of the detected loci, for example in *Arabidopsis* (Pfalz *et al.*, 2009) and in species of the genus *Solanum* (Bonierbale *et al*., 1994; Mutschler *et al*., 1996). Studies on trees have been far less abundant. In apple, Stoeckli *et al.* (2008) studied the relationship between aphid resistance and plant growth traits because, in addition to variations in plant

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chemistry, shoot growth characteristics may also influence plant susceptibility to pests. The authors identified significant QTLs for resistance to three aphid species and QTLs for plant shoot length and stem diameter. However, they found no relationship between the QTLs for the two kinds of traits.

Myzus persicae (Sulzer), the green peach aphid, feeds on numerous cultivated plant species and transmits several viruses across the world. It also has long been a model organism for studying the genetic adaptations of aphids to alterations their environment such as insecticide treatments. Genetic plant resistance represents another strong, human-imposed selection pressure on modern agroecosystems. In France, several sources of resistance to *M. persicae* have been identified in its primary host plant, the peach, *Prunus persica* (L.) Batsch (Rosaceae). Two single dominant genes, *Rm1* and *Rm2*, have been identified and mapped in the cultivars 'Weeping Flower Peach' and 'Rubira', respectively (Monet and Massonié, 1994; Pascal *et al.*, 2002; Lambert and Pascal, 2011). They confer strong antixenosis resistance, a mechanism that prevents plant colonisation (Sauge *et al*., 1998). The gene *Rm1* has been introgressed into a variety of fruit germplasms; however, its durability may be problematic if it is being relied upon in a variety of cultivars that are potentially planted over a large geographical area.

In accession P1908 of *Prunus davidiana* (Carr.) Franch, a wild species closely related to peach, QTLs linked to resistance to several diseases have been identified on different genetic linkage maps (Foulongne *et al*., 2003; Rubio *et al*., 2010). This species is partially resistant to *M. persicae*. Reduced aphid population growth rates (antibiosis) have been observed in the orchard, and this observation was verified in the laboratory (Sauge *et al*., 1998). Moreover, this trait was found to vary quantitatively in a segregating population derived from P1908 (Pascal, unpublished data). However, the direct cause of the resistance remains unknown.

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The first aim of this study was to identify and map QTLs controlling resistance to *M. persicae* in *P. davidiana* and to characterise their individual influence on resistance. For this, the development of aphid colonies and plant leaf curling responses were evaluated in an F_1 mapping population obtained from an interspecific cross between *P. persica* and *P. davidiana.* Our second aim was to identify parts of the *P. davidiana* genome influencing another key character involved in the plant-insect interaction, namely aphid probing and feeding behaviour. Aphids have evolved a highly specialised way of feeding. Their stylet mouthparts navigate through the cuticle, epidermis, mesophyll and cell walls to reach the phloem sieve elements, where they take up nutrients (Pollard, 1973). Identifying plant tissues where unfavourable cues are first perceived by the aphid provides a way of connecting variations in physical and chemical attributes of plants to behavioural and physiological consequences on the aphid. Using the same mapping population, we conducted a detailed analysis of aphid probing and feeding behaviour using the electrical penetration graph (DC-EPG) technique (Tjallingii, 1988), which allows us to discern, in real time, the location and activities of aphid stylets during probing, including their salivation into sieve elements and uptake of phloem sap.

We investigated the underlying genetic architecture of traits linked to aphid population growth and plant damage and identified several DNA markers associated with resistance loci. Next, by looking for colocation between the genetic determinants of plant resistance and those for aphid feeding behaviour, we evaluated the accuracy with which electrical penetration graphs estimated the level of plant suitability for the insect. Armed with this information, we attempted to generate assumptions regarding the nature of the physiological plant factors driving the decline of the aphid population.

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Materials and Methods

Mapping population

The study was carried out on an F_1 mapping population of 73 hybrids obtained from an interspecific cross between *Prunus persica* cv. 'Summergrand' clone S3971 and *Prunus davidiana* clone P1908. This population is referred to as SD for 'Summergrand' × *P. davidiana*, and it was designed to segregate for resistance to several peach pathogens and insect pests, including *M. persicae*. The yellow nectarine 'Summergrand' is the *M. persicae*-susceptible parent and P1908 is the resistant parent. Each genotype was clonally replicated by grafting onto GF305 peach seedlings and the mean genotype values were used for QTL analysis.

Plant resistance assessment

The SD population was assessed for resistance in two independent trials carried out in spring in Avignon, southern France (43°91′N, 4°85′E, and 24 m altitude). Resistance was assessed by means of a controlled infestation in the greenhouse on two-month-old saplings (trial 1) and under an insect-proof shelter on two-year-old trees (trial 2). The trees were cultivated in 1-L pots (saplings) or 50-L containers (two-year-old trees) containing a commercial horticultural mix (De Baat Substrate, Coevorden, The Netherlands). They were watered daily with a commercial solution containing micronutrients (Soluplant, Duclos International, Lunel Viel, France). Temperatures in the greenhouse were maintained at 23 ± 5°C. Temperatures under the shelter varied between 8°C and 18°C.

Ecologists usually believe that plant traits that reduce the detrimental effect of herbivores fall into two broad categories: resistance traits, which reduce herbivory, and tolerance traits,

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which reduce the impact of herbivory on plant fitness. Therefore, we used the development of aphid colonies (COL) as a measure of resistance, and the leaf curling response (CURL), which potentially reduces fruit production by disturbing leaf photosynthesis, was used as a measure of tolerance. Plant tolerance to chewing herbivores generally depends on insect abundance (via, for example, the physical loss of leaf area). But on the contrary, in the case of aphids, it has already been observed that the activation of plant defences could be independent of herbivore density. Thus, we defined two different criteria for plant resistance assessment. COL was scored from 0 = no aphids to 5 = all apices colonised by numerous aphids and CURL was scored from 0 = no curling to 5 = all apices curled using a well-established linear ordinal scale based on Pascal *et al*. (2002).

In trial 1, one apterous adult aphid was placed on the terminal apex of each tree. As the experiment proceeded, lateral axes developed so that the scoring took into account several growing shoots. In trial 2, one apterous adult aphid was placed on 5 growing shoots of each tree. The trees were assessed once a week over a three-week period in trial 1 (Trial 1 COL-wk1, Trial 1 CURL-wk1, Trial 1 COL-wk2, Trial 1 CURL-wk2, Trial 1 COL-wk3 and Trial 1 CURL-wk3) and over a two-week period in trial 2 (Trial 2 COL-wk1, Trial 2 CURL-wk1, Trial 2 COL-wk2 and Trial 2 CURL-wk2). A total of 10 notations were used to perform the QTL analysis. Each trial was stopped when the 'carrying capacity' was reached (aphid overcrowding) on the more susceptible trees. Two replicates per genotype were tested in trial 1, and three replicates were tested in trial 2.

The resistance phenotyping performed in trial 1 was carried out with a clone established from a single female collected in early spring from a producing peach tree in Avignon. The resistance phenotyping performed in trial 2 was conducted with a mixture of aphid clones that were also collected in Avignon, but from several other peach trees. The aphids used in each trial were retrieved from distinct genetic populations, because under a temperate climate, *M.*

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persicae host-alternates between herbaceous secondary host plants and the peach (its primary host) where sexual reproduction occurs, giving rise to genetic recombination. The aphids collected in early spring were clonal progeny of several fundatrices hatched from sexually produced eggs and, thus, are genetically different. For both trials, the mass rearing of aphids was conducted on seedlings of the susceptible peach cv. GF305 in a room maintained at 19°C and a 18:6 h photoperiod. Under these conditions, aphids reproduce parthogenetically.

Aphid probing and feeding behaviour

The probing and feeding behaviour of *M. persicae* on the SD population was studied using the DC-EPG technique (Tjallingii, 1988). In this technique, the aphid and its host plant are included in an electrical circuit. The penetration of the aphid stylet in the plant modifies the voltage of the signal, and different waveforms reveal information about the propagation of the stylet through the apoplast, the piercing of mesophyll cells, the secretion of watery saliva and the concurrent ingestion of phloem sap. The monitoring setup and protocol were the same as those described by Sauge *et al*. (2006). Recordings were made simultaneously on 6 plants. Each day, 18 insect/plant genotype combinations were recorded (3 series of 4-h recordings at 8:00 a.m., 13:00 p.m. and 17:00 p.m.). Each plant genotype was tested at each of the 3 times of day. Thirteen to 15 recordings per genotype were made. We performed the recordings in spring and used the same aphid clone as the one used in resistance trial 1.

Due to the high number of recordings required, the trees were not all grafted at the same time in order to assure that they were equally developed when the aphid behaviour was recorded. Six batches of 180-185 plants, each composed of 2 to 3 replicates of each genotype, were grafted approximately every 3 weeks. Recordings within a batch were performed at random on trees that were 30-35 cm high. In order to take into account the effect of the period of recording, data processing was necessary before calculating the EPG phenotype mean for

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each genotype. First, we calculated a "batch" effect as the difference between the mean of all individuals (all replicates for the 73 genotypes) over all batches and the mean of all individuals of each batch. Then, to correct for this "batch" effect when calculating the value of each individual, we subtracted this "batch" effect from the value taken by each individual of the batch. Finally, we calculated the mean values per genotype.

Five waveforms were scored: np (non-penetration), ABC (secretion of gelling saliva and pathway activities corresponding to the progress of the stylet in the plant tissues), E1 (secretion of watery saliva into the sieve element), E2 (passive ingestion of phloem sap with concurrent watery salivation) and F (derailed stylet mechanics). Seventeen EPG parameters were calculated from each EPG recording and analysed (Table 1).

Genotyping and mapping procedure

Due to the low heterozygosity of 'Summergrand', the 'Summergrand' map was not completed. Consequently, it was not used in this study. A P1908 genetic linkage map derived from the SD population had been previously developed and used for other purposes. Because the linkage groups (G) were mainly composed of RAPD markers not useful for comparative mapping, the coverage of the map was improved by adding SSR (single sequence repeat) loci. SSR analysis and map construction were performed using the same SSR primer pairs and procedures as in Rubio *et al*. (2010). In brief, a set of 278 SSR primer pairs developed from several *Prunus* species were first screened for polymorphism in both parents. The SSRs used for mapping were then chosen from among those polymorphic between the parents and heterozygous in *P. davidiana* or from their location in the almond (*Prunus dulcis* L.) cv. 'Texas' × peach cv. 'Earlygold' (T × E) reference map for *Prunus* (Genome Database for Rosacea - http://www.bioinfo.wsu.edu/gdr) or in other published *Prunus* genetic maps. Linkage analysis was performed using Mapmaker/exp version 3.0 software (Lincoln *et al*.,

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1992). Linkage groups were established using a critical logarithm of the odds (LOD) threshold >8 and a recombination fraction of 0.30. Marker distances were calculated using the Kosambi mapping function (Kosambi, 1944). Departures from the 1:1 ratio expected with this type of population were tested using chi-square goodness-of-fit on segregation data (P<0.05). Map figures were drawn using the MapChart software (Voorrips *et al*., 2002).

Statistical analysis

The descriptive statistics were computed using the R statistical software (R Development Core Team, 2006). The mean observed values for each genotype were used to compute correlations between the COL and CURL resistance traits and EPG parameters. Phenotypic data obtained from the observation of plant resistance *vs* susceptibility to *M. persicae* were suitable for QTL analysis without preliminary processing as they were recorded as a score. Aphid probing and feeding behavioural traits were recorded as a frequency or duration measure and showed rather large values for distribution skew. Skew values were optimally reduced after applying a square root transformation to the parameters GBSP-2, EPAA-5, PPFS-2, PPFS-3 and PPFS-4. For the other parameters, we checked that the distribution of genotype means did not deviate significantly from normality (Anderson-Darling's test, P < 0.05) and we carried out our analyses on the untransformed data. Broad-sense heritability (h) of the genotypic mean values was estimated using the formula $h^2 = \sigma^2_g/(\sigma^2_g + \sigma^2_e/n)$, where σ^2_g is the genotypic variance, σ^2_e is the environmental variance (error effects) and n is the number of replicates. The variance components were based on a mean square analysis of variance (ANOVA).

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QTL analysis

Using both phenotypic and EPG data, QTL detection was performed by composite interval mapping (CIM) with Windows QTL-Cartographer V2.5 software (Wang *et al*., 2007). In addition, a non-parametric test based on the Kruskal-Wallis (KW) methodology, which is more robust for data deviating from normality, was performed using the MapQTL 5.0 program (Van Ooijen *et al*., 2004). For KW tests, a significance threshold of 0.5% was used as recommended by Van Ooijen *et al*. (2004) to declare putative QTLs, but a less stringent threshold of 1% was considered when QTLs were also detected with CIM. For CIM, a 1,000 permutation test was performed for each cycle and each trait in order to estimate the most appropriate LOD threshold to declare a putative QTL (type-I error $\alpha = 0.05$), and co-factors were selected by forward-backward stepwise regression. The likelihood value for the presence of a QTL was estimated as the point where the LOD score was found to be maximised, and a 95% confidence interval was assessed from this point that had been decreased by 1 LOD unit. The phenotypic variation explained was estimated for each QTL (R^2).

Results

Characterisation of phenotypic traits

Considerable phenotypic variation in the development of aphid colonies and leaf curling responses was found in the SD population (Table 2). The difference between the minimum and maximum values recorded for these two phenotypic traits was similar in the two different trials, with slightly higher means in trial 1. Globally, the data showed that the distributions were close to normal with a high broad-sense heritability (>0.5) indicating that the phenotypic variation in these traits has a genetic basis.

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The SD population also segregated markedly for a number of aphid probing behaviour traits deciphered from the electronic recordings. The difference between the minimum and maximum values recorded for the EPG parameters varied from a mean of 2.8-fold for most parameters to a mean of 8.3-fold for parameters associated with the time spent in phloem sap ingestion (PPFS-2, PPFS-3 and PPFS-4) (Table 2). In addition, the broad-sense heritability of most traits was moderate to high, varying from 0.42 to 0.87; the only exceptions were GBSP-5 and EPAA-6 (h^2 = 0.32 and 0.36 respectively).

Within a trial and for each scoring time, four of a total of five possible associations between COL and CURL scores were significant (Pearson's correlation coefficient, *P*-value < 0.001), suggesting that the two criteria measuring the detrimental effect of aphids on the trees were not entirely independent. Of a total of ten possible associations among all of the COL scores, five were significant (*P*-value < 0.01). For the CURL scores, all ten correlations were significant (*P*-value < 0.001), indicating that the results were globally consistent across scoring times and trials.

Examination of the correlations between resistance scores and EPG parameters (Table 3) revealed that the relationship between the two kinds of traits was more pronounced in the trial conducted on two-year-old trees than in the trial conducted on saplings. Moreover, aphid probing and feeding behaviour was better related to the level of aphid colonisation and leaf damage in the late than in the early scoring times. There was a positive correlation between the level of plant susceptibility and the persistence of phloem sap ingestion (PPFS-2, PPFS-3 and PPFS-4), and a specific significant negative correlation between the intensity of the leaf curling response (Trial 1 CURL-wk3, Trial 2 CURL-wk1 and Trial 2 CURL-wk2) and the frequency of watery salivation (EPAA-2). Virtually no significant genetic correlations were detected between the resistance scores and any of the seven EPAA variables that characterise the ease of phloem access.

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Genetic map

The basic number of chromosomes in *Prunus* is n=8. The genetic linkage map of *P. davidiana* P1908 consists of eight linkage groups, as expected. Those linkage groups in which QTLs were identified are shown in Fig. 1. Forty-five SSRs were mapped in the entire population for a total of 48 loci (41% of the initial set of markers). They were distributed among seven of the eight linkage groups, and they significantly improved map coverage, in particular G3, which was insufficiently covered. This allowed better map anchorage to the T × E *Prunus* reference map and to the numerous published *Prunus* maps. The map of *P. davidiana* is now composed of 165 markers. They are distributed among 122 loci (1.35 markers/locus) that contain 90 codominant markers. The map length was estimated to be 89% by comparison with published *Prunus* maps with some disparities (from approximately 100% for G1, G5 and G6 to 68% for G8). No significant differences in locus order were observed between the map of *P. davidiana* and these *Prunus* maps. The total map length is 545.8 cM for a mean distance between loci of 4.47 cM. Only three markers at the top of G1 significantly deviated from their chi-square expectations at $P<0.05$.

QTLs for aphid colony development and leaf curling response

QTL analysis was performed for each of the trial/trait combinations. The empirical threshold computed was comprised between 2.34 (Trial 1 COL-wk2) and 2.51 (Trial 1 CURL-wk3). A total of seven regions were identified by either one or both methods used (KW or CIM). These QTLs were named *MP.SD-1.1*, *MP.SD-2.1*, *MP.SD-3.1*, *MP.SD-4.1*, *MP.SD-5.1*, *MP.SD-5.2* and *MP.SD-8.1* according to the aphid name, the population (SD), the linkage group on which they were identified and a number. Their locations and effects are summarised in Table 4, and their positions in the linkage groups are shown in Fig. 1. For each

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QTL considered, the *P. davidiana* allele whose additive effect has a negative sign (Tables 4 and 5) was named B and the other was named A in order to highlight that they belong to opposite chromosomes. The alleles that were linked to decreased aphid colonisation and/or leaf curling are hereafter referred to as "resistance alleles".

The major resistance QTL (*MP.SD-3.1*) was identified on G3 close to the *AG106* and *AG50B* RFLP markers for all of the trial/trait combinations, and both methods showed a very high degree of consistency among evaluations and traits. This QTL accounted for the greatest contribution to resistance (R^2=14.6 to 43.1) in all the trial/trait combinations except for Trial 1 CURL-wk1, with LOD scores between 3.7 and 13.8. Its individual contribution to the variance compared to the total variance explained by the model was 50.5% on average. Among the other QTLs, *MP.SD-5.1* and *MP.SD-4.1* accounted for the greatest contribution with R^2 from 14.2 to 23.6 and from 8 to 16.4, respectively; they were detected for several trial/trait combinations and were detected in both trials. On G5, a marker (*ssrPaCITA21*) was found to be more likely associated with leaf curling (in 4 out of 5 CURL traits, but only in 1 COL trait). The associated QTL (*MP.SD-5.2*) was mainly detected with the Kruskal-Wallis test. As this test does not allow us to define a confidence interval, it was considered different from *MP.SD-5.1*. No obvious relationship was found between the other QTLs and a particular trait (CURL or COL).

QTLs for aphid probing and feeding behaviour

Nine quantitative trait loci affecting characteristics of aphid probing and feeding behaviour were identified (Table 5, Fig. 1). They were named according to the nomenclature previously defined (see previous section), and the same name as was used for the QTLs regulating aphid colony development and leaf curling responses was used when both confidence intervals overlapped or when markers close to the QTL peaks were in the confidence interval of one of

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the QTLs. Their locations and effects are summarised in Table 5 and Fig.1. The empirical threshold computed was between 2.27 (GBSP-2) and 2.48 (EPAA-5). The individual phenotypic variation explained by the QTLs (R^2) ranged from 8.7% (*MP.SD-2.1*) to 18.4% (*MP.SD-3.1*) for LOD scores between 2.43 and 4.43, and the total variance explained by the model (R^2_t) was between 21.2 % and 48.5%.

Among the nine loci related to EPG parameters, six mapped to regions of the genome where *P. davidiana* alleles had favourable effects as measured by decreased aphid colonisation and reduced leaf curling responses (*MP.SD-2.1, MP.SD-3.1*, *MP.SD-4.1*, *MP.SD-5.1*, *MP.SD-5.2* and *MP.SD-8.1*). *MP.SD-3.1*, *MP.SD-4.1* and *MP.SD-5.2* were the three most frequently detected QTLs in the resistance evaluation trials (10, 6 and 5 times, respectively).

There was a remarkable association between the resistance allele (referred to as allele B) *AG106*, the nearest marker to the major QTL *MP.SD-3.1*, and lower mean values of several parameters linked to phloem sap ingestion activity (PPFS-2, PPFS-3 and PPFS-4) (Table 6). This allele decreased both the median non-penetration period (GBSP-3) and the time needed to initiate the first ingestion of phloem sap (EPAA-7). This allele also caused a significant elevation in the frequency of watery salivation events (EPAA-2). An elevation in the frequency of watery salivation events was also observed for *MP.SD-5.2*, a QTL that was mainly detected by CURL scores in the resistance trials. At this QTL, the allele of the flanking marker *ssrPaCITA21* (referred to as allele A) was found to be related to a lower level of leaf distortion, and it co-locates with a genomic region that increases the mean value of EPAA-2 (allele A: 7.2 *vs*. allele B: 6.6, *P*-value = 0.035). This result corroborates the significant negative correlation that we specifically detected between the tolerance scores and EPAA-2. For *MP.SD-4.1*, the resistance allele at marker CC133C (referred to as allele A) decreased the mean duration of a probe (GBSP-2) (allele A: 21.2 *vs*. allele B: 25.2, *P*-

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value<0.01), a result consistent with the overall reduction in ingestion activity on resistant hybrids.

On G6, two QTLs for attributes of aphid probing behaviour were found that do not co-locate with QTLs controlling the development of aphid colonies or leaf curling responses. One QTL was identified in the region harbouring marker *PC9,* whereas another one was detected close to *UDP-412*. They were named *MP.SD-6.1* and *MP.SD-6.2,* respectively. The signs of their additive effects are opposing (−12.87 and 0.94, respectively), indicating that these *P. davidiana* alleles linked to the expression of their respective attributes are in opposition.

No QTL was detected for GBSP-5, GBSP-6, EPAA-1 or EPAA-6. These are four parameters that mainly reflect the ease of progress through the mesophyll and vascular parenchyma prior to phloem acceptance.

Discussion

The ability to link, in a plant-aphid interaction, quantitative genetic resistance with variations in insect behaviour during the exploration of plant tissues, the search for phloem vessels and the ingestion of sap (as monitored by EPG) is unprecedented. We detected seven significant QTLs for the development of aphid colonies and the leaf curling response, each explaining 6.1 to 43.1% of the phenotypic variation. Nine QTLs influencing *M. persicae* probing and feeding behaviour were also identified. Strikingly, most of them mapped to the same location in the *P. davidiana* genome as those identified for resistance. This result suggests that there is a clear genetic basis for the phenotypic relationship observed between EPG variables (which were collected within the first 4 hours of the plant-aphid interaction) and aphid abundance and plant damage criteria (which were evaluated over a 2 or 3-week period after the start of plant

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infestation). The estimates of the correlations among the two kinds of traits were moderate, but they fell within the same range as Hawthorne and Via (2001) observed between indicators of performance (fecundity) and habitat choice (behavioural acceptance of the host plant) within F_2 progeny of a cross between pea aphids specialised on alfalfa and pea aphids specialised on red clover. Using an aphid genetic linkage map, these authors then showed co-localisation between the QTL complexes underlying the two traits.

The EPG technique is a technology that has been increasingly employed since the early 1980s by aphid biologists and plant geneticists. However, most studies have been based on comparisons of a few susceptible and resistant accessions or cultivars bearing heterogeneous genetic backgrounds. Therefore, the exact genetic relationship between plant resistance phenotypes and aphid behavioural abilities to detect and exploit nutrient sources often remained unknown. After the pioneering work of van Helden and Tjallingii (1993), only a few studies have been conducted, either on mutant plants (Hunt *et al.,* 2006) or on near isogenic lines differing only in an aphid resistance gene (Kaloshian *et al*., 2000; Klingler *et al.,* 2005). For tree species, the delay required to obtain such lines is a key problem. Here, we took advantage of the ability to vegetatively propagate peach trees and the development of molecular data to establish, for the first time, a comparative plant genetic linkage map of QTLs controlling host acceptance (phloem access and suitability) and resource use (aphid population growth). Our QTL analysis provides a starting point for a better understanding of the plant defence system, which in turn may reveal the mechanisms that can give rise to host resistance adaptations in aphid populations. Using the EPG method, Caillaud and Via (2000) studied the mechanisms of plant discrimination and rejection by host races of pea aphids, and they provided evidence for the influence of feeding behaviour on ecological specialisation.

MP.SD-3.1, the major resistance QTL in *P. davidiana,* is clearly associated with EPG signals, indicating a phloem-based resistance that efficiently impairs the persistence of sap

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uptake and thus aphid population growth. In general, co-located QTLs either correspond to distinct, closely linked genes or to a single gene with a pleiotropic effect on several traits influenced by the same physiological process. *MP.SD-3.1* is likely a single locus controlling a mechanism restricting food acquisition, causing it to have a strong negative impact on aphid population dynamics. A higher-resolution analysis based on a denser linkage map is required to verify this hypothesis.

Aphids have the ability to overcome phloem-associated defence systems by injecting watery saliva, which is thought to prevent sieve-tube occlusion occurring either by plugging with proteins or by callose deposition (Will *et al.,* 2007). In several studies, authors have measured longer periods of watery salivation (E1 waveform) on resistant plants (i.e., Caillaud *et al*., 1995). By measuring the rate of success in phloem sap collection by stylectomy, Caillaud and Niemeyer (1996) provided evidence suggesting that phloem sealing elements play a role in host plant resistance to cereal aphids. In the present study, aphids feeding on hybrids harbouring the resistance alleles at *MP.SD-3.1* and *MP.SD-5.2* produced a high number of watery salivation events, which might help to secure the flow of nutrients by eliminating plant phloem defences.

The possibility that features of epidermal or mesophyll cells negatively affect aphid performance on *P. davidiana* can probably be ruled out. No significant QTL was identified for traits characterising aphid stylet activity in plant tissues other than phloem vessels. We even found a reduction in the time to initiate phloem sap ingestion at locus *MP.SD-3.1*. In the case of the resistance QTL *MP.SD-1.1*, for which no colocation with QTLs linked to EPG parameters could be detected, it can be hypothesised that the underlying mechanism (such as aphid intoxication by a plant toxin) works in a delayed fashion that is not reflected in short-term behavioural interference. Conversely, *MP.SD-6.1* and *MP.SD-6.2* are two QTLs that exhibit EPG parameter-specific effects, indicating that plant-aphid interactions are probably

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subtly regulated and cannot be reduced to a mere relationship between physical or chemical characteristics of the plant and host suitability.

The size of our mapping population prevented us from precisely mapping the QTL positions and from quantifying the effects of those for which the explained variance was low. However, our findings are in agreement with results present in the literature regarding the number of QTLs for resistance against herbivorous insects that are normally detected (Nunez-Farfan *et al.*, 2007). Genotype × Environment interactions are another important aspect that has to be taken into account when trying to verify the relevance of identified QTLs. QTLs whose expression differs across environments seem to be the rule rather than the exception in tree species (Asíns *et al.,* 1994; Emebiri *et al.,* 1998; Garcia *et al.,* 2000). Concerning the influence of growth characteristics of the host plant on resistance to aphid infestation, the effects of neighbouring tree infestation levels and/or different climatic conditions at the experimental site may impede the identification of genetically based resistance (Stoeckli *et al.,* 2008). In this study, significant QTLs common to both trials were detected, although the test conditions varied (greenhouse *vs*. shelter, saplings *vs*. two-year-old trees, monoclonal aphid colony *vs*. a mixture of genotypes for infestation). This demonstrates their robustness and suggests that the resistance genes underlying the detected QTLs are likely to have functions across plant developmental stages and to act against a range of aphid genotypes.

As the routine use of marker-assisted selection (MAS, i.e., the determination of the segregation of a gene of interest by the presence/absence of a molecular marker instead of by phenotype) notably depends on resistance QTLs that can be introgressed into commercial cultivars, the observed consistency of the QTLs over several trials, including the aphid probing behaviour assay, reinforces the potential of MAS to facilitate traditional peach breeding. Further validations involving different mapping populations, multilocale trials and evaluations over a period of years would improve estimates of the genetic architecture of

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aphid resistance in *P. davidiana*. Similar work has already been performed in this species for resistance to powdery mildew (Foulongne *et al.*, 2003).

In summary, we identified several QTLs for resistance to *M. persicae* and for aphid probing and feeding behaviour in the wild peach *P. davidiana*. We demonstrated that most of them exhibit colocation. A QTL of major effect confers a clear phloem-specific antibiosis resistance. In light of these results, comprehensive studies of the sieve tube's physiology and a survey of the metabolome of phloem sap are warranted to expand our knowledge of the mode of action of resistance in *P. davidiana*. In addition to plant tissue characteristics, it is likely that emitted volatile organic compounds also participate in the defence arsenal in this species (Staudt *et al*., 2010). The study of QTL co-localisation with candidate genes may help to further clarify the attributes of resistance from a functional point of view. The recent sequencing of the peach genome (http://www.rosaceae.org/peach/genome) provides promising prospects for the future.

Conflict of interest

The authors declare no conflict of interest.

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Fig. 1 Locations of quantitative trait loci (QTLs) for plant resistance and *Myzus persicae* probing and feeding behaviour on the genetic linkage map of *Prunus davidiana* 1908. SSR loci added to the former map (Foulongne *et al.,* 2003) are underlined. Only linkage groups (Gs) in which QTLs have been detected are shown. QTLs detected for resistance traits are indicated by an arrow, and those related to aphid feeding behaviour are indicated by a ball on the left on the linkage groups opposite to the peak marker. For ease of viewing, confidence intervals are not shown, and some dominant markers that co-locate with co-dominant markers have been discarded from the map. The QTL with the strongest effect is emphasised with a thicker arrow.

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Table 1 Electrical penetration graph (EPG) parameters used to characterise the aphid probing and feeding behaviour

EPG parameter	*Abbreviation*
General Behaviour during Stylets Progression towards the sieve tubes (GBSP)	
1. Number of probes during the recording	GBSP-1
2. Mean duration of a probe (min)	GBSP-2
3. Median duration of a non-penetration period (sec)	GBSP-3
4. Total duration of non-penetration (min)	GBSP-4
5. Median duration of a pathway period within a probe (sec)	GBSP-5
6. Total duration of derailed stylet mechanics (min)	GBSP-6
Ease of Phloem Access and Acceptance (EPAA)	
7. Time to first sieve element salivation (min)	EPAA-1
8. Number of sieve element salivation periods	EPAA-2
9. Total duration of sieve element salivation (min)	EPAA-3
10. Percentage of time spent in sieve element salivation after the beginning of the first sieve element salivation period (%)	EPAA-4
11. Time elapsed between first sieve element salivation and first sustained* phloem sap ingestion (min)	EPAA-5
12. Total duration of sieve element salivation before first sustained phloem sap ingestion (min)	EPAA-6
13. Time to first phloem sap ingestion (min)	EPAA-7
Persistence of Phloem Feeding and phloem Suitability (PPFS)	

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14. Number of phloem sap ingestion periods	PPFS-1
15. Total duration of phloem sap ingestion (min)	PPFS-2
16. Percentage of time spent in phloem sap ingestion after the beginning of the first phloem sap ingestion period (%)	PPFS-3
17. Mean duration of a phloem sap ingestion period (min)	PPFS-4

*, longer than 10 min

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Table 2 Distribution of traits within the *Prunus persica* × *Prunus davidiana* F_1 mapping population

Trait	*No. of clones per genotype*	*Minimum value*	*Maximum value*	*Mean*	*SD*	*Heritability*	*Skew*	*Kurtosis*
Plant resistance phenotype (COL, development of aphid colonies ; CURL, leaf curling response; wk, week)								
Trial 1 COL-wk1	2	0.6	3.2	2.114	0.553	0.69	-0.095	0.281
Trial 1 CURL-wk1	2	0	3	1.353	0.789	0.82	-0.017	0.792
Trial 1 COL-wk2	2	1.2	4	2.491	0.700	0.87	-0.000	0.573
Trial 1 CURL-wk2	2	0.2	3.6	2.023	0.906	0.82	-0.164	1.600
Trial 1 COL-wk3	2	1.8	4	2.997	0.619	0.62	0.003	0.308
Trial 1 CURL-wk3	2	0.8	4	2.505	0.864	0.76	-0.072	1.262
Trial 2 COL-wk1	3	1.1	4.3	3.200	0.795	0.74	-0.334	1.114
Trial 2 CURL-wk1	3	0.5	4.3	2.089	0.905	0.73	0.178	1.639
Trial 2 COL-wk2	3	1.2	3.6	2.766	0.499	0.79	-0.070	0.264
Trial 2 CURL-wk2	3	0.8	4.5	2.479	0.872	0.83	0.188	1.339
Aphid probing and feeding behaviour (refer to Table 1 for explanation)								
GBSP-1	13 to 15	8	18.8	13.58	2.27	0.75	0.335	71.60
GBSP-2*	13 to 15	3	6.7	4.8	0.656	0.56	0.125	0.722
		8.9	*44.5*	*23.77*	*6.47*	*0.51*	*260.6*	*7948*
GBSP-3	13 to 15	49.9	135.4	75.24	17.39	0.55	5295.7	409716
GBSP-4	13 to 15	13.3	41.8	24.19	5.63	0.65	89.5	3510
GBSP-5	13 to 15	156.4	427.3	263.4	67.2	0.32	132418.7	52414833
GBSP-6	13 to 15	20.9	54.2	27.53	10.62	0.42	164.4	41717
EPAA-1	13 to 15	25.9	97.7	58.7	14.19	0.43	732.6	130819
EPAA-2	13 to 15	4.6	10.4	6.97	1.13	0.70	0.476	6.03
EPAA-3	13 to 15	13.8	35.6	24.2	5.4	0.63	25.9	2319
EPAA-4	13 to 15	7.5	19.4	13.35	2.74	0.49	0	0
EPAA-5*	13 to 15	8.71	13.62	11.12	1.10	0.70	0.388	4.10
		75.8	*185.6*	*124.6*	*24.15*	*0.70*	*-596.5*	*950789*
EPAA-6	13 to 15	8.65	34.48	18.44	5.19	0.36	72.3	2450
EPAA-7	13 to 15	56.2	159	103.2	23.83	0.71	3069.6	920826
PPFS-1	13 to 15	1.1	4.2	2.8	1.32	0.61	0.094	0.559

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PPFS-2*	13 to 15	0.92	7.97	5.10	1.26	0.61	0.006	10.98
		0.9	*63.5*	*27.65*	*12.71*	*0.61*	*1497*	*101871*
PPFS-3*	13 to 15	0.095	0.692	0.44	0.756	0.84	-0.0003	0.0005
		0.9	*48*	*20.26*	*8.96*	*0.84*	*0.0005*	*0.0003*
PPFS-4*	13 to 15	0.614	5.417	3.09	0.756	0.87	-0.046	1.53
		0.4	*29.4*	*10.13*	*4.73*	*0.87*	*114.3*	*3004*

Trial 1, saplings; Trial 2, two-year old trees; *, Square root transformation has been applied prior to QTL analysis (original data are in italics). Values are those used in QTL analysis. All data are from mean genotype values for each trait.

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Table 3 Pearson's coefficients of correlation between traits of plant resistance and EPG parameters used to characterize the aphid probing and feeding behavio

73 genotypes of the *Prunus persica* × *Prunus davidiana* F_1 mapping population

EPG parameters	*Trial 1 COL-wk 1*	*Trial 1 CURL-wk 1*	*Trial 1 COL-wk 2*	*Trial 1 CURL-wk 2*	*Trial 1 COL-wk 3*	*Trial 1 CURL-wk 3*	*Trial 2 COL-wk 1*	*Trial 2 CURL-wk 1*	*Trial 2 COL-wk 2*	*Trial 2 CURL-wk 2*
GBSP-1	**0.302***	−0.044	0.192	0.069	−0.028	−0.050	−0.077	−0.058	−0.084	−0.159
GBSP-2	−0.217	0.115	−0.124	0.016	0.098	0.105	**0.252***	0.213	**0.309****	**0.270***
GBSP-3	0.070	0.114	0.050	0.107	**0.317****	**0.284***	0.040	**0.305****	**0.252***	**0.299***
GBSP-4	0.190	−0.078	0.143	0.040	−0.013	0.038	0.016	0.045	−0.013	−0.062
GBSP-5	**−0.304***	−0.076	−0.230	−0.136	0.021	0.032	−0.186	0.003	−0.063	−0.060
GBSP-6	0.053	0.143	0.047	0.033	0.046	0.024	0.085	0.167	0.138	0.157
EPAA-1	0.051	0.053	0.090	0.058	0.137	0.159	−0.016	0.153	0.089	0.168
EPAA-2	−0.056	−0.076	−0.191	−0.168	−0.203	**−0.316****	−0.022	**−0.326****	−0.198	**−0.316****
EPAA-3	0.002	0.052	−0.052	0.013	0.055	−0.061	0.123	−0.049	−0.034	0.034
EPAA-4	0.011	0.073	−0.026	0.033	0.111	−0.005	0.122	−0.003	−0.007	0.078
EPAA-5	0.104	0.057	0.051	0.025	−0.007	−0.023	−0.001	0.011	−0.127	−0.153
EPAA-6	0.112	0.108	0.100	0.082	0.105	0.040	0.099	0.024	0.045	0.064
EPAA-7	0.149	0.003	0.129	0.034	0.073	0.057	−0.048	**0.234***	0.063	0.155
PPFS-1	−0.097	−0.029	−0.137	−0.079	−0.130	−0.179	−0.051	−0.221	−0.122	−0.210
PPFS-2	**−0.236***	−0.028	−0.073	−0.017	0.117	0.145	0.044	0.135	**0.321****	**0.262***
PPFS-3	−0.188	−0.034	−0.039	−0.008	0.206	0.205	0.036	**0.268***	**0.359****	**0.368*****
PPFS-4	−0.141	0.004	0.002	0.025	**0.267***	**0.302***	0.080	**0.342****	**0.369*****	**0.447*****

Trial 1, saplings; Trial 2, two-year old trees; COL, development of aphid colonies ; CURL, leaf curling response; EPG parameters, refer to Table 1 for explanation; *, $P<0.$

$P<0.001$. Coefficients calculated with the mean value per genotype averaged on two to three replications for resistance traits and on 13 to 15 replications for EPG parameters.

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Table 4 Summary characteristics of quantitative trait loci (QTLs) detected for each resistance score dataset by Kruskal-Wallis test (KW) and composite interval mapping (CIM). Only QTLs equal to or above the empirical threshold are listed for CIM

			KW			*CIM*					
Trial/trait combination	*QTL*	*G*	*Locus*	*Pos*	*P-value*	*Locus*	*Pos*	*LOD*	*Effect*	R^2	R^2_t
Trial 1 COL-wk1	*MP.SD-3.1*	3	AG50B	30.1	$<5\times10^{-3}$	AG50B	30.5 (26-36)	5.00	0.54	20.9	48.7
	MP.SD-4.1	4	AG12	57.5	$<5\times10^{-3}$	AG12	57.6 (53-63.5)	4.11	−0.50	16.4	
Trial 1 CURL-wk1	*MP.SD-1.1*	1	ssrPaCITA5	31.5	$<5\times10^{-3}$	-	-	-	-	-	64.5
	MP.SD-2.1	2	-	-	-	I13-134	29.7 (25-34)	5.01	−0.61	15.0	
	MP.SD-3.1	3	AG106	32.6	$<1\times10^{-4}$	AG50B	30.5 (27-40)	3.66	0.63	14.6	
	MP.SD-4.1	4	CC133C	47.6	$<5\times10^{-3}$	UDAp-471B	65.6 (60-66.5)	2.49	−0.46	8.0	
	MP.SD-5.1	5	-	-	-	BPPCT026	12.2 (8-17)	7.02	−0.78	23.6	
	MP.SD-5.2	5	ssrPaCITA21	26.7	$<1\times10^{-4}$	-	-	-	-	-	
Trial 1 COL-wk2	*MP.SD-3.1*	3	AG50B	30.1	$<1\times10^{-4}$	AG50B	30.5 (29-35)	9.29	0.92	39.7	59.6
	MP.SD-4.1	4	-	-	-	AG12	57.6 (52-62)	5.13	−0.59	16.0	
	MP.SD-5.2	5	ssrPaCITA21	26.7	$<5\times10^{-3}$	-	-	-	-	-	
Trial 1 CURL-wk2	*MP.SD-3.1*	3	AG50B	30.1	$<5\times10^{-3}$	AG50B	30.5 (27-35)	6.45	0.95	23.3	57.0
	MP.SD-4.1	4	-	-	-	AG12	57.6 (52-62)	3.47	−0.65	11.2	
	MP.SD-5.1	5	UDP-401	15.7	$<5\times10^{-4}$	UDP-401	15.7 (11-24)	4.21	−0.69	14.2	
Trial 1 COL-wk3	*MP.SD-3.1*	3	AG106	32.6	1×10^{-4}	AG106	34.6 (29-39)	6.38	0.71	31.1	45.0
Trial 1 CURL-wk3	*MP.SD-3.1*	3	AG106	32.6	1×10^{-4}	AG106	32.6 (31-39)	6.08	0.85	23.6	59.0
	MP.SD-5.2	5	ssrPaCITA21	26.7	1×10^{-4}	AC53	21.3 (15-28)	5.77	−0.75	18.6	
Trial 2 COL-wk1	*MP.SD-3.1*	3	AG50B	30.1	$<1\times10^{-4}$	AG106	32.6 (30-39)	10.22	0.97	36.0	61.0
	MP.SD-5.1	5	UDP-401	15.7	$<5\times10^{-3}$	-	-	-	-	-	
Trial 2 CURL-wk1	*MP.SD-1.1*	1	ssrPaCITA5	31.5	$<5\times10^{-3}$	-	-	-	-	-	56.3
	MP.SD-3.1	3	AG106	32.6	5×10^{-4}	AG106	32.6 (30-39)	8.22	1.10	35.7	
	MP.SD-5.1	5	UDP-401	15.7	$<5\times10^{-3}$	BPPCT026	10.2 (6-17)	7.02	−0.78	16.5	
	MP.SD-5.2	5	ssrPaCITA21	26.7	$<1\times10^{-4}$	-	-	-	-	-	
Trial 2 COL-wk2	*MP.SD-3.1*	3	AG50B	30.1	$<1\times10^{-4}$	AG106	32.6 (29-37)	8.44	0.56	27.1	55.1
	MP.SD-4.1	4	UDAp-471B	65.6	$<5\times10^{-3}$	UDAp-471B	65.6 (55-66.5)	3.84	−0.39	11.7	
Trial 2 CURL-wk2	*MP.SD-3.1*	3	AG106	32.6	$<1\times10^{-4}$	AG106	32.6 (31-36)	13.79	1.18	43.1	71.6
	MP.SD-4.1	4	AG12	57.5	$<5\times10^{-3}$	-	-	-	-	-	

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MP.SD-5.2	5	ssrPaCITA21	26.7	$<1\times10^{-3}$	-	-	-	-	-
MP.SD-8.1	8	-	-	-	PC34A	35.8 (29-37.7)	2.43	0.46	6.1

Trial 1, saplings; Trial 2, two-year old trees; G, Linkage group; Locus, marker showing strongest association with trait; Pos, Position of the QTL at peak in cM (in brackets I
confidence interval for CIM); P-value, Significance of the association between the QTL and the closest marker; LOD, Logarithm of odds score under composite interval mappi
Individual contribution to the variance in a trait accounted for by the QTL (%); R^2_t , Total variance explained by the model (%).

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Table 5 Summary characteristics of quantitative trait loci (QTLs) detected for each EPG parameter dataset by Kruskal-Wallis test (KW) and composite interval mapping (CIM). Only QTLs above the empirical threshold are listed for CIM

			KW			*CIM*					
EPG parameter	*QTL*	*G*	*Locus*	*Pos*	*P-value*	*Locus*	*Pos*	*LOD*	*Effect*	R^2	R^2_t
GBSP-1	*MP.SD-2.1*	2	-	-	-	CFFn	31.7 (26-39)	2.88	−2.28	16.2	26.4
GBSP-2	*MP.SD-4.1*	4	CC133C	47.6	$<5\times10^{-3}$	-	-	-	-	-	
	MP.SD-5.1	5	UDP-401	15.7	<0.01	UDP-401	15.8 (11-24)	2.27	−0.45	11.1	34.5
GBSP-3	*MP.SD-3.1*	3	-	-	-	AG106	32.6	2.46	12.87	13.3	27.7
	MP.SD-6.1	6	PC9	33.6	$<5\times10^{-3}$	PC9	33.6 (28.5-41)	2.43	−12.5	12.0	
GBSP-4	*MP.SD-8.1*	8	AC12	37.5	<0.01	PC34A	35.3 (30-37.7)	3.03	−4.96	16.9	26.9
EPAA-2	*MP.SD-3.1*	3	AG106	32.2	<0.01	AG106	32.6 (27-42)	2.37	−0.79	11.2	35.8
	MP.SD-5.2	5	-	-	-	ssrPaCITA21	28.9 (25-32)	2.72	1.20	15.1	
EPAA-3	*MP.SD-8.1*	8	PC34A	35.8	$<5\times10^{-3}$	PC34A	35.2 (24-37.7)	2.62	4.18	14.9	21.2
EPAA-4	*MP.SD-8.1*	8	PC34A	35.8	$<1\times10^{-3}$	PC34A	33.3 (22-37.7)	3.11	0.02	18.2	25.8
EPAA-5	*MP.SD-1.2*	1	-	-	-	O6-1500	47.6 (41-59)	2.67	0.86	13.4	35.1
	MP.SD-6.2	6	-	-	-	UDP-412	68.1 (61-74)	3.37	0.94	16.3	
EPAA-6	*MP.SD-3.1*	3	AG106	32.2	<0.01	AG106	32.6 (27-41)	3.02	18.26	13.3	36.2
PPFS-1	*MP.SD-3.1*	3	-	-	-	AG106	32.6 (20-43)	2.41	−0.46	10.2	38.1
PPFS-2	*MP.SD-3.1*	3	AG106	32.2	<0.01	AG106	32.6 (30.5-40)	2.71	0.88	11.6	37.7
PPFS-3	*MP.SD-2.1*	2	CFFn	32.4	$<5\times10^{-3}$	CFFn	32.6 (26-37)	2.46	0.06	8.7	48.5
	MP.SD-3.1	3	AG106	32.2	$<1\times10^{-4}$	AG106	32.6 (31-38)	4.43	0.09	18.4	
PPFS-4	*MP.SD-2.1*	2	CFFn	32.4	$<5\times10^{-3}$	CFFn	31.7 (27-36)	3.30	0.86	12.5	41.2
	MP.SD-3.1	3	AG106	32.2	$<1\times10^{-4}$	AG106	32.6 (31-38)	3.63	0.60	15.7	

G, Linkage group; Locus, marker showing strongest association with trait; Pos, Position of the QTL at peak in cM (in brackets LOD-1 confidence interval for CIM); *P*-value, Significance of the association between the QTL and the closest marker; LOD, Logarithm of odds score under composite interval mapping; R^2, Individual contribution to the variance in a trait accounted for by the QTL (%); R^2_t , Total variance explained by the model (%).

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Table 6 Genotype class means for *Myzus persicae* probing and feeding behavioural traits at the marker closest to the major resistance effect QTL, *MP.SD-3.1*. Plants containing allele B from *P. davidiana* displayed lower COL and CURL scores than those containing allele A

EPG parameter	*Flanking marker*	*Allele B (resistance allele)*	*Allele A*	*Effect*	*P-value*
GBSP-3	AG106	68.6	79.9	−	0.007
EPAA-2		7.4	6.6	+	0.007
EPAA-7		96.1	108.3	−	0.045
PPFS-2		23.0	31.1	−	0.012
PPFS-4		7.7	11.1	−	0.001
PPFS-3		15.4	21.9	−	0.003

For the allele linked to resistance, + indicates an increasing effect and − indicates a decreasing effect on the feeding and probing behavioural attribute; *P*-values are from Student's *t*-test; homogeneity of variance was checked using Levene's test; for square root-transformed data, the means of the original data are given.

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