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QTL analysis of quality traits in an advanced backcross between *Prunus persica* cultivars and the wild relative species *P. davidiana*

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Abstract Genetic control of the different attributes involved in peach quality has been investigated in an advanced backcross population derived from a cross between *Prunus davidiana* clone P1908, a wild parent with poor agronomic performance, and a commercial variety, Summergrand. A total of 24 physical and biochemical traits were investigated. Quantitative trait loci (QTLs) were detected for all the traits studied. We identified alleles from *P. davidiana* with agronomically favorable effects regarding fruit and stone sizes, sugar and acid concentrations and red flesh coloration, in clear contrast to its phenotype. We identified three main regions of the genome where alleles from *P. davidiana* had negative effects on multiple traits. In other regions, co-locations of QTLs with opposite effects on quality traits were also detected. We discuss the nature of these co-locations in the light of the probable physiological mechanisms involved. Strategies to cope with negative

correlations between favorable traits and co-locations of *P. davidiana* alleles with negative effects on quality traits and positive effects regarding resistance to powdery mildew are discussed from a breeding point of view.

Introduction

A lack of diversity in germplasm limits long-term progress in plant breeding. Wild germplasm has long been used to improve resistance to pests and diseases. However, the use of wild germplasm often results in the introgression of unfavorable agronomic traits. A common marker-assisted method applied when introgressing resistance factors from wild germplasm consists in suppressing the greater percentage of the wild parent genome, apart from those regions harboring resistance factors, in order to ensure good agronomic performance. This method does not exploit the potential genetic resources of wild germplasm which might improve commercial varieties in terms of agronomic traits such as fruit quality or recently evidenced environmental adaptation, even when the phenotype of the wild species is inferior. Thus studies on tomato have proved that alleles from wild species may improve some plant habit and fruit quality traits (Fulton et al. 1997; Bernacchi et al. 1998). Studies in rice (Moncada et al. 2001) and barley (Pillen et al. 2003) also support this view. As a result, a targeted elimination of regions from the wild parent with negative agronomic effects may constitute a valid alternative to suppressing the majority of the wild genome that does not harbor resistance factors.

A major problem encountered when breeding for quality lies in negative correlations between favorable traits. For instance, in the tomato, fruit size and soluble sugar concentrations are two quality traits which are often negatively correlated. In many cases, this results from co-locations of quantitative trait loci (QTLs) with opposite horticultural effects (Fulton et al. 1997; Causse et al. 2002). Because it is often necessary to search for resistance sources among exotic germplasms, horticulturally unfavorable co-locations can also be expected

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between resistance factors and fruit quality QTLs. Studies in barley have reported negative effects on malting quality or yield of the introgression of mildew resistance factors (Swanston 1987; Thomas et al. 1998), but to our knowledge, such co-locations between quality traits and factors of resistance to pests and diseases have not been extensively investigated. In the current context of the development of varieties with good levels of both agronomic quality and resistance to pests and diseases, such investigations may be relevant. Whether co-locations correspond to linkages between genes or to a unique gene with a pleiotropic effect is of interest in terms of breeding. Further genetic studies are often required to resolve this difficulty.

In this paper, we describe the QTL analysis of fruit agronomic and quality traits in an advanced backcross breeding population derived from an interspecific cross (*Prunus persica* × *P. davidiana*). *P. davidiana* (hereafter referred to as D) is a wild relative of the cultivated peach, and a source of resistance to several major pests and diseases (Smykov et al. 1982). D fruit quality is very poor due to a high stone-to-flesh ratio, low sugar and high malic acid concentrations (Moing et al. 2003). D has been used in a peach resistance breeding program and the advanced backcross population has been characterized for powdery mildew resistance (Foulongne et al. 2003). Preliminary observations of fruit characteristics in this population revealed horticulturally favorable transgressions, suggesting the possible interest of D in the improvement of fruit quality traits, but until now no efforts have been made to take advantage of this factor.

During this study, we examined variations in quality traits within the breeding population and identified correlations between them. We mapped the QTL for those traits focusing particularly upon the effect of alleles from the wild parent *P. davidiana*, in order to further evaluate the possible interest of wild germplasm to improving fruit traits. Lastly, we analyzed the co-locations of QTLs between fruit traits and resistance factors to powdery mildew, and determined whether some might be of value to improving cultivated peach varieties.

Materials and methods

Genetic material

A clone of the wild species *P. davidiana* (P1908) (D) was crossed with the yellow-fleshed nectarine *P. persica* cv. Summergrand (S), developed in the late 1970s, to obtain an F₁ progeny. A single F₁ hybrid (SD40) selected for its good level of resistance to powdery mildew (*Sphaerotheca pannosa* var. *persicae*) was backcrossed to S to produce a BC₁ progeny. A mixture of pollen from BC₁ hybrids was used to fertilize another commercial peach variety Zéphyr (Z). This white-fleshed nectarine, more recent than S, was chosen for its high fruit quality. Considering the *persica* versus *davidiana* origin of alleles, the population obtained was similar to a BC₂ progeny. For the sake of concision, this progeny will be referred to as BC₂ throughout this paper. In fact, it differs from a BC₂ population in two ways: firstly, because although the *persica* parents used to produce the BC₁ and BC₂ populations both produce tasty fruit and are thus similar when compared with D, they are not identical. Secondly, their heterozygosity is expected to be low but not null, as is the case in other peach cultivars (Aranzana et al. 2003). The possible genotypes at one locus in the BC₂ progeny are presented in Table 1.

One hundred and sixty-two individuals from the BC₂ population and the three parents D, S and Z, were grafted onto GF305 seedling rootstocks and planted in a completely randomized design (5 m between rows and 1.1 m within rows) with one tree per genotype, in the orchard of the Avignon INRA Research Centre (southern France) in 2001. They were grown under normal conditions of irrigation, fertilization and pest control. Environmental sources of variations between genotypes and between fruits within a genotype were minimized by carrying out heavy fruit thinning.

Fruits were considered as mature and were harvested when they no longer grew, had softened, and could easily be picked. Maturity dates ranged from the end of June to the beginning of October, depending on the genotypes.

Fruit traits

Fruit traits were measured for 105 BC₂ genotypes, S, and Z in 2001, and for 140 BC₂ genotypes, S, Z and D in 2002. Eighty-nine genotypes were common to both years.

Table 1 Possible genotypes at a single locus in SD, BC₁ and BC₂ progenies

D×S	SD40×S		BC ₁ ×Z		
	D ₁	D ₂	D ₁	S ₁	D ₁ S ₁ S ₂
SD			BC ₁		BC ₂
S ₁	D ₁ S ₁	D ₂ S ₁	S ₁	D ₁ S ₁ S ₁ S ₁	Z ₁ D ₁ Z ₁ S ₁ Z ₁ S ₂ Z ₁
S ₂	D ₁ S ₂	D ₂ S ₂	S ₂	D ₁ S ₂ S ₁ S ₂	Z ₂ D ₁ Z ₂ S ₁ Z ₂ S ₂ Z ₂
SD40 genotype is coded D ₁ S ₁ at one locus			Possible gametes from BC ₁ progeny		
			D ₁ (1/4)	S ₁ (1/2)	S ₂ (1/4)

Blooming date (Bloom), maturity date (Matu), fruit polar diameter (FPolarD), fruit cheek diameter (FCheekD), fruit suture diameter (FSutureD), stone cheek diameter (SCheekD), fruit mass (FMass), stone mass (SMass), dry flesh mass content (DFMC), soluble solid content (SSC), sucrose (Suc), glucose (Glu), fructose (Fru), sorbitol (Sor), total sugar (TSugar) contents, and malic acid (Mal), citric acid (Cit), quinic acid (Qui), shikimique acid (Shi), total acid (TAcid) contents were measured both years. Red skin coloration (SRColor), skin speckle (SSpeckle), red flesh coloration (FRCOLOR), juiciness (Jui) and sweetness (Swe) were scored in 2002 only.

The full blooming date, expressed in Julian days, corresponded to the day when most flowers were fully opened at the same time. The maturity date, in days after full bloom, corresponded to the averaged harvest day. Peach versus nectarine was noted for each BC₂ tree. For red skin coloration, skin speckles, red flesh coloration, juiciness and sweetness, a mean score by genotype was calculated from the scores given by four non-trained persons for each harvested fruit. Red skin coloration was rated on a 0–100% scale. The presence or absence of skin speckles was noted for nectarines only. Red flesh coloration was scored on a three-point scale corresponding to whole red flesh, half red flesh and non-red flesh. A distinction was made between juicy and non-juicy fruits. Sweetness was rated as poor, medium or high.

The SSC was determined using a digital refractometer. Fruit flesh was cut into small pieces, frozen immediately and then stored (–70°C) for further chemical analysis. Frozen fruit flesh samples were then powdered and prepared as described by Wu et al. (2003). Sugar (sucrose, glucose, fructose and sorbitol) and acid (malic, citric, quinic and shikimic) concentrations were then measured under the conditions described by Gomez et al. (2002) and Wu et al. (2002), respectively.

Genotyping

Foulongne et al. (2003) developed a map for BC₂ progeny with 41 RFLP markers of the D genome, based on the study of 263 individuals. This map covered most of the LG1, LG2, LG3, LG4, LG5 and LG6 linkage groups as defined in the almond (cv. Texas) × peach (cv. Earlygold) *Prunus* reference map (Aranzana et al. 2003). However, gaps remained on LG2, LG3 and LG6, only half of LG7 was covered and LG8 was not represented. We chose SSRs and AFLPs markers of the D genome on the basis of an F₂ related map (Foulongne et al. 2003) and of the T×E reference map to improve map coverage. Owing to the origin of the BC₂ population, we wanted to be able to detect possible QTLs corresponding to substitution effects between S or Z alleles. Markers making it possible to distinguish among S alleles or among Z alleles were also scored.

SSR genotyping was performed according to the method described by Cipriani et al. (1999). Twenty-three *Prunus* SSRs previously developed by Cipriani et al.

(1999), Testolin et al. (2000), Sosinski et al. (2000) and Aranzana et al. (2003) were analyzed for polymorphisms. Most of these were already positioned on the ‘Texas’ almond × ‘Earlygold’ peach (T×E) map.

AFLP genotyping was carried out as described by Lu et al. (1998), with *EcoRI*–*MseI* primer combinations. We used two combinations (E31-M47 and E31-M52) coded respectively CFF and CFM, that had provided most AFLP markers in the regions of the F₂ related map where gaps remained on the BC₂ map.

Statistical analysis

Mean observed values for each genotype and year were used to compute correlations between traits and between 2001 and 2002 for each trait.

New markers of the D versus S genome were positioned on the existing linkage map (Foulongne et al. 2003) using Mapmaker (Lander et al. 1987). Considering the particular origin of the BC₂ progeny, recombination rates between successive markers were then calculated, assuming identical recombination rates for the BC₁ and BC₂ generations, using the maximum likelihood method as described in Allard (1956). The Kosambi function was used to convert the recombination units into genetic distances. SSR markers already positioned on the T×E map made it possible to assign some of the few markers of S and of Z alleles to the eight linkage groups.

Since correlations for most traits between 2001 and 2002 were low, QTL detection was carried out separately for each year using trait values averaged by genotype for each corresponding year. Software performing QTL detection with composite interval mapping approaches did not allow us to take full account of the particular origin of the progeny studied. Therefore, QTL detection was performed using a forward multiple linear regression of the phenotypic values on the genotype at each of the molecular markers, with S-Plus software (MathSoft, Cambridge, Mass., USA). The most likely QTL position corresponded to the locus of the marker exhibiting the strongest association with the trait. A threshold of significance of 5% was chosen to declare a putative QTL. Possible digenic epistatic interactions were analyzed using two-way analysis of variance for all pair-wise combinations of marker loci. They were considered to be significant if the probability associated with the *F*-test exceeded one out of the number of marker pairs considered.

Results

Phenotypic distribution and correlation between fruit traits

Correlations between years ranged from 0.93 for the maturity date to 0.35 for the total sugar concentration (Table 2). In view of the relatively low correlations

between years, the data from 2001 and 2002 were analyzed separately.

The distributions of fruit traits were very similar for the 2 years. For this reason, only those obtained in 2002 are shown in Fig. 1. Several fruit traits, i.e., blooming date,

Table 2 Correlation coefficients between fruit traits measured for 103 genotypes in 2001 (above diagonal) and 140 in 2002 (below diagonal) for BC₂ progeny. The diagonal indicates the correlation coefficients between the 2 years and 88 genotypes were common to the 2 years. The correlation coefficients were calculated with one mean value per genotype averaged on three to five replications. *Bloom* blooming date, *Matu* maturity date, *FMass* fruit mass, *SMass*

stone mass, *DFMC* dry flesh mass content, *SSC* soluble solid content, *Suc* sucrose, *Glu* glucose, *Fru* fructose, *Sor* sorbitol, *TSugar* total sugar contents, *Mal* malic acid, *Cit* citric acid, *Qui* quinic acid, *Shi* shikimique acid, *TAcid* total acid content, *SRColor* red skin coloration, *FRCColor* red flesh coloration, *Jui* juicy, *Swe* sweetness

Traits	Bloom	Matu	FMass	SMass	DFMC	SSC	Suc	Glu	Fru
Bloom	0.63***	0.00	0.12	0.12	-0.02	-0.10	-0.03	-0.11	0.25**
Matu	0.07	0.93***	0.21*	0.14	-0.02	-0.21*	-0.33***	0.32**	0.28**
FMass	0.29***	-0.05	0.48***	0.63***	-0.38***	-0.34***	-0.04	-0.38***	-0.12
SMass	0.32***	-0.19*	0.62***	0.61***	-0.08	-0.12	-0.10	-0.17	-0.07
DFMC	0.19*	-0.02	0.17	0.12	0.49***	0.87***	0.60***	0.28**	0.28**
SSC	0.17	-0.20*	0.25**	0.09	0.88***	0.49***	0.71***	0.08	0.18
Suc	0.14	-0.02	0.31***	0.15	0.75***	0.75***	0.41***	-0.27**	-0.07
Glu	-0.03	0.18*	-0.40***	-0.31***	0.12	0.00	-0.14	0.43***	0.65***
Fru	0.20*	0.11	0.09	0.05	0.12	0.06	-0.13	0.32***	0.70***
Sor	0.23**	0.36***	0.14	0.04	0.71***	0.56***	0.58***	0.19*	0.12
TSugar	0.21*	0.11	0.22**	0.08	0.83***	0.75***	0.88***	0.22**	0.26**
Mal	0.09	-0.04	-0.06	-0.06	0.26**	0.16	0.14	0.16	0.04
Cit	-0.15	-0.35***	-0.31***	-0.12	-0.19*	-0.23**	-0.27**	0.09	0.03
Qui	0.16	-0.36***	0.26**	0.14	0.44***	0.46***	0.45***	-0.05	0.15
Shi	0.08	-0.21*	0.02	0.04	0.20*	0.23**	0.13	0.07	0.11
TAcid	0.04	-0.25**	-0.08	-0.04	0.20*	0.14	0.10	0.11	0.07
SRColor	-0.10	-0.24**	0.07	-0.12	0.01	0.08	0.20*	-0.05	-0.18*
FRCColor	0.03	-0.02	-0.26**	-0.18*	0.04	0.03	0.14	-0.01	-0.22**
Jui	0.07	-0.07	0.21*	0.19*	0.01	0.02	0.05	-0.02	0.18*
Swe	0.19*	-0.05	0.37***	0.29***	0.40***	0.45***	0.43***	-0.03	0.29***

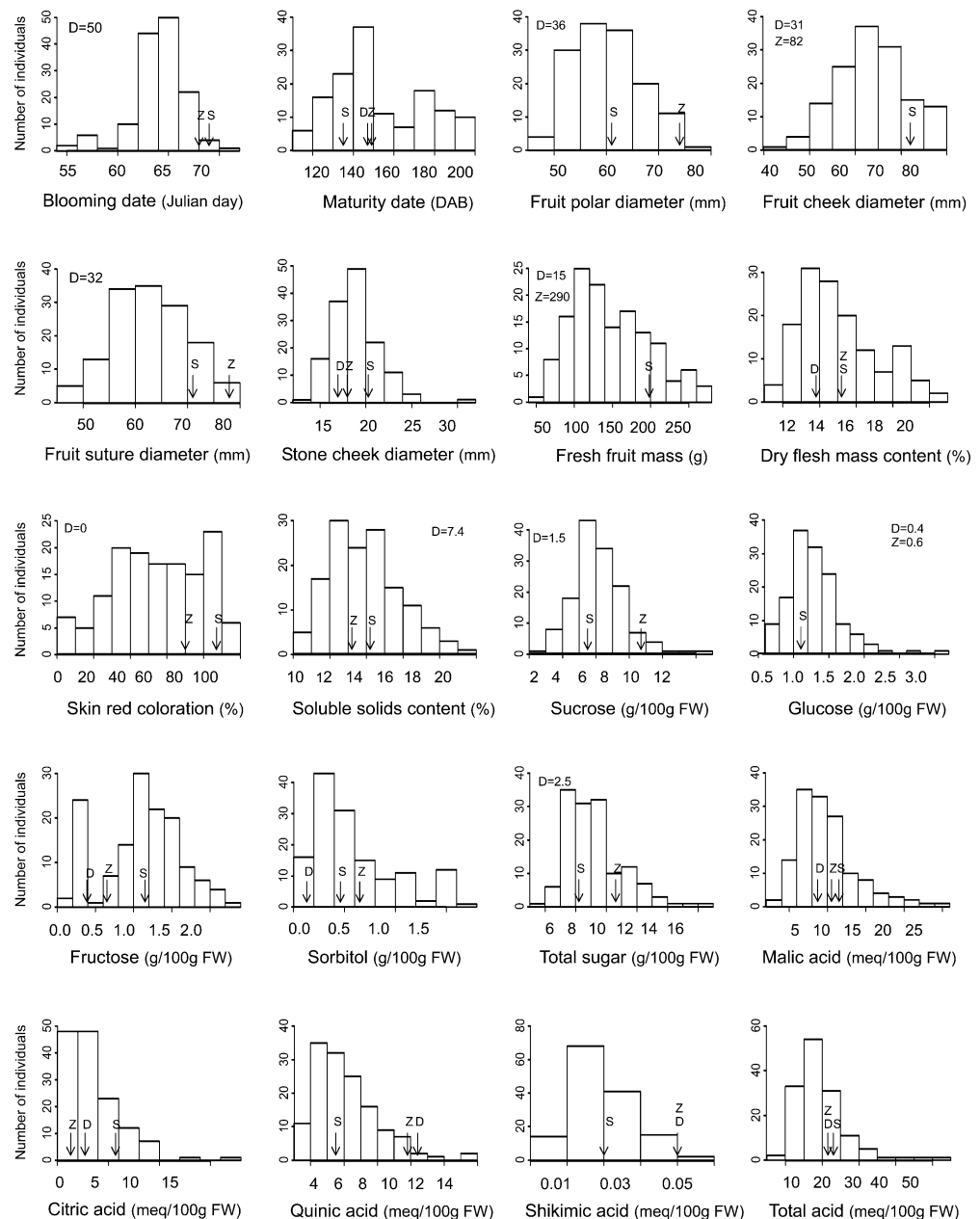
Traits	Sor	TSugar	Mal	Cit	Qui	Shi	TAcid	SRColor	FRCColor	Jui
Bloom	-0.01	0.02	-0.09	-0.11	0.04	-0.04	-0.09	-	-	-
Matu	0.41***	0.03	0.18	-0.18	0.02	0.20*	0.07	-	-	-
FMass	-0.18	-0.20*	-0.22*	-0.25**	-0.15	-0.22*	-0.28**	-	-	-
SMass	-0.11	-0.16	-0.09	0.04	-0.10	-0.12	-0.07	-	-	-
DFMC	0.73***	0.81***	0.46***	-0.02	0.67***	0.36***	0.49***	-	-	-
SSC	0.61***	0.79***	0.33***	-0.10	0.65***	0.26**	0.36**	-	-	-
Suc	0.36***	0.78***	0.20*	-0.25**	0.59***	0.13	0.21*	-	-	-
Glu	0.33***	0.28**	0.23*	0.22*	0.15	0.24*	0.28**	-	-	-
Fru	0.33***	0.46***	0.08	0.04	0.36***	0.30**	0.23*	-	-	-
Sor	0.47***	0.75***	0.50***	-0.14	0.50***	0.26**	0.43***	-	-	-
TSugar	0.76***	0.35***	0.41***	-0.18	0.72***	0.31**	0.41***	-	-	-
Mal	0.22**	0.21*	0.56***	0.35***	0.46***	0.21*	0.94***	-	-	-
Cit	-0.30***	-0.26**	0.51***	0.72***	-0.06	-0.07	0.57***	-	-	-
Qui	0.16	0.43***	0.55***	0.24**	0.39***	0.66***	0.56***	-	-	-
Shi	0.03	0.16	0.29*	0.14	0.66***	0.47***	0.30**	-	-	-
TAcid	0.06	0.14	0.92***	0.74***	0.68***	0.40***	0.54***	-	-	-
SRColor	-0.13	0.07	0.15	0.19*	0.13	-0.06	0.19*	-	-	-
FRCColor	0.01	0.05	0.22**	0.35***	-0.01	-0.18*	0.25**	0.38***	-	-
Jui	-0.18*	0.05	0.04	0.02	0.23**	0.09	0.10	0.03	-0.10	-
Swe	0.31***	0.50***	-0.05	-0.27***	0.31***	0.16	-0.04	0.00	-0.21*	0.16

P*<0.05, *P*<0.01, ****P*<0.001

fruit diameters, sucrose, glucose, malic acid, quinic acid, shikimic acid and total acid, presented a typical normal distribution. For the maturity date, dry flesh mass content, sorbitol and fructose, a bimodal distribution was observed. The population exhibited considerable genotypic variations in all fruit traits. The full blooming dates of genotypes ranged from 20 February to 13 March. Many genotypes were transgressive for early and, above all, late maturity dates. Indeed, the maturity dates ranged from 30 June to 1 October in the BC₂ population, whereas the three parents ripened between 15 July and 7 August. As for fruit dimension and coloration traits, the BC₂ genotypes displayed broad variations but these did not exceed the parent values, whereas for the other traits transgressive segregants were observed for high values. The fruit size and mass of all genotypes were larger than those seen in D

fruits. Red skin coloration ranged from 0 to 100%. Thus, some genotypes displayed higher values than S but most of them had lower values than the commercial parents S and Z. Dry flesh mass content, soluble solid content and total sugar concentration exhibited marked variations ranging from 11 to 20%, 10.1 to 19.3% and 5.6 to 16.7 g/100 g FFM, respectively. Soluble solid contents reached higher values than for S and Z in nearly half the genotypes. Transgressive segregants were also observed for high concentration values of individual sugars (except sucrose), and for low concentration values of fructose. Malic acid and total acid concentrations in the three parents were close to each other while the population displayed broad variations in these concentrations, with many transgressive segregants for high and low levels. As for the other three individual acids, S differed significantly

Fig. 1 Distribution of peach fruit traits measured on 140 BC₂ progenies in 2002. The distribution was calculated using one mean value per genotype averaged on three to five replications. The values for the 'Summergrand' (S), 'Zéphyr' (Z) and *Prunus davidiana* (D) parents are indicated by arrows. The soluble solids content for D was obtained from Moing et al. (2003)



from the two other parents and the population displayed smaller variations than for malic acid concentrations.

The correlation coefficients between the fruit traits are shown in Table 2. Correlations including blooming date, maturity date or fruit and stone sizes were sometimes opposite in 2001 and 2002. In both years, strong positive correlations were observed between maturity date and sorbitol concentration, fruit mass and stone mass, while fruit mass was negatively correlated with glucose and citric concentrations.

Significant correlations between all variables concerning flesh composition (dry flesh matter content, soluble solid content and sugar and acid concentrations) were stable from one year to the other. High positive correlations were found between dry flesh mass content, soluble solid content and total sugar concentration. These three variables were all well correlated with sucrose, sorbitol and quinic acid concentrations. Sorbitol and sucrose concentrations on the one hand and glucose and fructose concentrations on the other hand were positively correlated. Individual acid concentrations were positively correlated with each other and with the total acid concentration. Most correlations between sugar and acid concentrations were weak.

QTL detection

A total of 69 new molecular markers (46 AFLP and 23 SSR) were analyzed to complement the existing genetic linkage map for the 162 BC₂ individuals. The 41 markers from the existing linkage map of the D versus S genomes along with 39 new markers were organized into eight linkage groups (LG1–LG8) corresponding to the eight peach chromosomes ($2n=2x=16$). The genetic map with 80 markers, differentiating D from S alleles, has a total length of 590 cM. Nine other AFLP markers for the D genome, for which few individuals possessed the D allele, could not be assigned to these linkage groups but could be grouped into three more groups (LG9–LG11). Because of the low heterozygosity of peach cultivars, only a few markers that made it possible to distinguish among S alleles and among Z alleles could be found. Seven SSR markers of S and six SSR markers of Z alleles were assigned to one of the eight linkage groups. Three and five AFLP markers of S and Z alleles, respectively, remained unlinked. We also mapped two phenotypic markers corresponding to the peach versus nectarine trait (G) and to the low versus high bimodal quantitative trait “fructose to glucose concentration ratio” (FRU). They were positioned on LG5 and LG1, respectively.

QTLs were detected for all the quantitative traits analyzed and for both years (Table 3, Fig. 2) and accounted for between 11 and 78% of the observed differences in variables. For eight traits analyzed, QTLs were detected in 2001 and 2002 at the same loci. Moreover, for seven traits analyzed QTLs were detected in 2001 and 2002 in the same regions, at the loci of

neighboring markers. We focused on these reproducible results throughout the paper.

With respect to the blooming date, QTLs were found for both years on LG1 and LG2. For both years, the same two QTLs were detected for maturity date and were strongly associated with the polymorphism for SSR UDP96-003 on LG4, corresponding to DNA polymorphism within both the S and Z genomes.

The markers linked with the six QTLs for fresh fruit mass, on linkage groups 1, 2, 4, 5 and 7, were also related to QTLs for fruit dimensions. A QTL with a high individual contribution (41%) was detected for stone cheek diameter on LG6. It was also detected for fresh stone mass in 2002, but with a weaker effect and smaller individual contribution (17%). In 2001, it was hardly detected for fresh stone mass, with an individual contribution of only 11%.

QTLs affecting glucose and fructose concentrations were co-located on LG2, LG4 and LG7. Two QTLs affecting total sugar concentration were found in the same region of LG1 in 2001 and 2002, but they were not associated with any QTL for individual sugar concentrations. The allele from D at these two QTLs had negative but not significant effects on all individual sugar concentrations. The QTLs for sucrose concentration were associated with QTLs for other individual sugar concentrations (LG7).

QTLs for the various individual acid concentrations were not co-located except in three regions. In the first two regions, QTLs linked to acidity were observed. Near marker CC8 on LG3, alleles from D tended to elevate malic, citric and total acid concentrations and to lower the shikimic acid concentration. Lastly, QTLs for quinic, malic and total acid concentrations were co-located on LG5, near the G marker, with alleles from D tending to lower these concentrations. QTLs for sweetness were detected on LG1 associated with FRU (“low-fructose” trait), on LG3 associated with a QTL for the shikimic acid concentration and on LG5, near the G marker, associated with QTLs for total sugar and acid concentrations. In all cases, D alleles negatively affected sweetness.

With respect to juiciness, QTLs were detected on LG4 and on LG7, with D alleles having a negative and positive effect, respectively. Near the QTL for juiciness on LG4, D alleles also had a negative effect on the soluble solid content and fresh mass. QTLs for skin and flesh red colorations were mapped in different regions of the genome except for the region located by a marker of S alleles. The others were detected on LG5 for red skin coloration and on LG1 and LG3 for red flesh coloration. Concerning skin speckle, three out of the four QTLs were associated with markers of Z and S alleles.

Discussion

For 15 traits studied, correspondences between one QTL for 2001 and 2002 were detected. For the other QTLs detected, year-to-year inconsistencies were observed. This

Table 3 Linkage group locations, effects and contributions of putative QTLs controlling fruit quality traits analyzed for two successive years. *LG* Linkage group. The locus is the marker showing strongest association with trait. The location of markers is given in cM quoted from the top of each linkage group. In the case of markers for S and Z, distances were not available. The *P*-value cited is the significance of the association between the QTL and the marker, while r^2 represents the individual contribution of one QTL

to the variations in a trait. Global r^2 represents the fraction of the total variation explained by the QTL. The effect represents the additive effect on the trait mean value of the presence of one allele at a marker by comparison with the presence of the second allele. In the case of a marker for the D genome, the effect quoted corresponds to the presence of the D allele instead of the peach allele. – and + indicates the direction of the additive effect

Traits	Year	LG	Locus	Location	<i>P</i> -value	Effect	r^2	Global r^2
Blooming date (Julian day)	2001	1	AG102	0.11	1.7e–05	–4.0492	0.16	0.27
		5	Pchgms4	0.45	0.00034	–3.7582	0.12	
		2	CC115	0.99	0.021	–2.472	0.02	
	2002	1	AG102	0.11	5.4e–06	–2.0322	0.16	0.45
		6	CFF12	0.68	1.9e–10	2.7775	0.09	
		4z	CFM8	NA	0.00086	1.2333	0.07	
Maturity date (DAB)	2001	1	CFF9	1.16	0.00036	–1.9708	0.06	0.39
		2	CC41b	1.01	0.00047	–1.7194	0.03	
		4z	UDP96-003	NA	3.5e–11	–30.7822	0.30	
	2002	4s	UDP96-003	NA	0.00033	–18.3278	0.04	0.53
		4z	UDP96-003	NA	0.0	–28.2213	0.35	
		4s	UDP96-003	NA	2.5e–07	–19.2542	0.08	
Fruit polar diameter	2001	2	AC6	0.34	0.0094	10.4701	0.06	0.18
		3	CC2	0.45	0.00083	13.8145	0.04	
		5	AG108	0.64	0.00087	5.6486	0.09	
	2002	7	CC63b	0.23	0.0012	–6.7515	0.08	0.33
		4	CC129	0.11	1.1e–06	–5.9971	0.14	
		1	CFF9	1.16	0.00018	–4.9678	0.08	
Fruit cheek diameter	2001	6	UDP96-001	0.11	0.0093	–3.2761	0.05	0.22
		5	AG108	0.64	0.00028	4.4593	0.04	
		4	CFF4	0.81	0.0056	–5.4889	0.09	
	2002	1	CFF2	0.26	0.0055	–5.9594	0.08	0.42
		6	CFF12	0.68	0.0034	5.6468	0.03	
		1	PC102	0.47	6.0e–06	–6.1807	0.11	
Fruit suture diameter	2001	4	CC3	0.44	2.6e–05	–7.6007	0.09	0.14
		2	CC115	0.99	6.9e–06	–6.6624	0.08	
		4z	CFM8	NA	0.0028	3.4119	0.08	
	2002	5	FG26	0.0	0.0013	–4.351	0.06	0.42
		1	CFF2	0.26	0.0087	–5.0016	0.07	
		5	AG108	0.64	0.0059	5.1445	0.06	
Stone cheek diameter	2001	1	PC102	0.47	2.1e–07	–6.3467	0.13	0.49
		4	UDP96-003	0.46	7.5e–07	–7.3196	0.12	
		2	CC115	0.99	1.5e–06	–6.3831	0.07	
	2002	5	FG26	0.0	0.0003	–4.3968	0.07	0.23
		6	PC60	0.60	0.0	3.8017	0.41	
		1	PC78	0.35	0.0049	–1.1431	0.03	
Fruit mass	2001	4	CC75	0.30	0.00082	–1.4382	0.03	0.46
		4	CFF4	0.81	0.0048	–22.1761	0.08	
		7	CFF11	0.28	0.0012	–29.9495	0.07	
	2002	5	AG108	0.64	0.00082	28.2234	0.06	0.23
		4	CC129	0.11	6.6e–05	–36.068	0.16	
		1	PC102	0.47	0.0034	–26.5104	0.12	
		e ^a	CFM6'-CFF16	5.4e–05	–29.1011	0.11		
			CFF4	0.81	1.5e–05	–36.2209	0.10	
			CC115	0.99	0.00031	–32.8536	0.06	

Table 3 (continued)

Traits	Year	LG	Locus	Location	P-value	Effect	r^2	Global r^2
Stone mass	2001	6	PC60	0.60	0.0055	1.2065	0.11	0.33
		8z	UDP96-019	NA	0.0012	-1.2827	0.09	
		3s	UDP97-403	NA	0.0072	1.1615	0.06	
		10	CFF20	NA	0.004	3.4999	0.05	
Dry flesh mass content	2002	6	PC60	0.60	5.0e-06	2.0015	0.17	0.44
		4	UDP96-003	0.46	2.7e-07	-2.968	0.12	
		e ^b	AG108-CFF6	0.00013	2.4962	0.11		
Soluble solid content	2001	1	PC78	0.35	1.4e-05	-2.0327	0.06	0.24
		5	AG108	0.64	1.9e-05	-0.0424	0.16	
Sucrose	2002	3z	UDP96-008	NA	0.0017	0.0237	0.07	0.14
		5	AG46	0.52	0.0016	-0.0145	0.09	
Glucose	2001	3	CC20	0.27	0.0047	0.0174	0.08	0.22
		5	AG108	0.64	0.00027	-2.7825	0.14	
		4	CC129	0.11	0.0023	-2.1866	0.09	
Fructose	2002	5	AG46	0.52	0.00077	-1.3737	0.09	0.19
		4	CC129	0.11	0.0093	-0.9838	0.05	
		2	CFM5	0.54	0.0079	-1.2667	0.04	
Sucrose	2001	7	Pchcms2	0.43	0.0088	-1.9089	0.07	0.13
		6	CFF8'	0.48	0.014	-1.3271	0.06	
Glucose	2002	7	CFF10	0.46	0.00024	-1.3989	0.11	0.21
		3	CC20	0.27	0.0056	1.1659	0.06	
		3s	UDP96-008	NA	0.01	-0.6724	0.06	
Fructose	2001	2	CC115	0.99	0.0008	0.5757	0.09	0.19
		7	Pchcms2	0.43	0.0045	0.5851	0.06	
		4	CFF4	0.81	0.0002	0.2689	0.15	
		5	FG26	0.0	0.0037	0.2276	0.11	
Sorbitol	2002	7	AG104	0.31	0.0079	0.2025	0.08	0.32
		5z	Pchgms4	NA	0.0083	-0.1653	0.07	
		1	PC102	0.47	2.9e-15	-1.3395	0.46	
		4s	UDP96-003	NA	0.0072	-0.3714	0.06	
		4z	UDP96-003	NA	0.006	-0.3135	0.05	
Fructose	2002	2	CC125	1.04	0.0037	0.4274	0.03	0.65
		1	PC102	0.47	0.0	-0.9454	0.55	
		2	CFM5	0.54	0.018	0.1993	0.17	
		4	CFF4	0.81	0.0022	0.2083	0.03	
Sorbitol	2001	7	Pchcms2	0.43	0.0008	0.3101	0.03	0.17
		4z	UDP96-003	NA	0.0016	-0.5915	0.10	
		2	AC6	0.34	0.0063	0.6841	0.088	
Total sugar	2002	5	AG46	0.52	0.0064	-0.2327	0.05	0.11
		4z	UDP96-003	NA	0.0067	-0.1839	0.05	
Total sugar	2001	1	PC35	0.75	0.00065	-2.9313	0.15	0.22
		6	CFF8'	0.48	0.007	-1.8949	0.10	
		5	AG46	0.52	0.00069	-1.3628	0.08	
Malic acid	2002	1	CFF17	0.96	0.009	-1.0726	0.05	0.13
		5	AG46	0.52	0.012	-3.6393	0.07	
		6	CFF8'	0.48	0.0074	-3.6229	0.06	
		4z	UDP96-003	NA	0.011	-2.8275	0.04	
		3	CC8	0.60	0.0028	2.8335	0.09	
Malic acid	2002	2	Pchgms1	0.86	0.025	-2.2599	0.05	0.15
		5	AG46	0.52	0.023	-1.8621	0.04	

Table 3 (continued)

Traits	Year	LG	Locus	Location	P-value	Effect	r^2	Global r^2	
Citric acid	2001	1	PC35	0.75	7.3e-06	3.2232	0.16	0.26	
		3	UDP96-008	0.64	0.00034	2.697	0.09		
	2002	4z	UDP96-003	NA	2.5e-06	2.0134	0.10	0.27	
		3	UDP96-008	0.64	1.1e-05	2.5946	0.07		
Quinic acid	2001	7	AG104	0.31	0.0019	1.58	0.06	0.26	
		1	PC30	0.58	0.00012	-1.8121	0.13		
		7	CFF10	0.46	0.003	-1.7262	0.08		
	2002	6s	BPPCT025	NA	0.006	-1.721	0.04	0.22	
		4z	UDP96-003	NA	0.004	0.9515	0.09		
		1	CFF17	0.96	0.0068	-1.131	0.05		
Shikimic acid	2001	5z	Pchgms4	NA	0.00039	1.3121	0.05	0.21	
		5	Pchgms4	0.45	0.0056	-1.2387	0.01		
		3	PC13	0.67	0.0047	-0.0074	0.08		
	2002	6	CFM6'	0.83	0.0033	0.0056	0.07	0.15	
		3s	UDP97-403	NA	0.024	-0.0044	0.06		
		8s	UDP96-019	NA	0.012	-0.0062	0.07		
Total acid	2001	4	CC138	0.49	0.0078	0.006	0.06	0.13	
		3	UDP97-403	0.08	0.03	-0.0064	0.04		
	2002	2	CFM5	0.54	0.0098	-7.0227	0.07	0.18	
		5	AG46	0.52	0.0089	-5.4355	0.07		
Peach/nectarine Red skin coloration	2002	3	CC8	0.60	2.2e-05	6.9602	0.11	0.18	
		4z	UDP96-003	NA	0.00072	3.8421	0.06		
Skin speckle	2002	5	AG108	0.64	0.0	-0.8434	0.78	0.78	
		5	AG108	0.64	1.6e-07	-25.1686	0.21		0.29
		9s	CFF1	NA	0.00073	-13.8408	0.10		
Red flesh coloration	2002	6	CFF12	0.68	0.0006	0.3382	0.10	0.27	
		6s	BPPCT025	NA	0.0043	-0.3629	0.07		
		3z	UDP96-008	NA	0.0047	0.259	0.06		
		11z	CFM4'	NA	0.019	0.4134	0.03		
Juiciness	2002	3	UDP96-008	0.64	3.3e-12	0.8179	0.26	0.43	
		1	CFF14	0.20	0.0002	0.3526	0.13		
		9s	CFF1	NA	0.0095	-0.2209	0.04		
Sweetness	2002	4	CFM10	0.17	1.5e-06	-0.4488	0.16	0.23	
		7	CC63b	0.23	0.00092	0.3699	0.05		
Sweetness	2002	1	PC102	0.47	4.7e-05	-0.6088	0.13	0.21	
		3	UDP97-403	0.08	0.0084	-0.6342	0.06		
		5	AG46	0.52	0.0087	-0.3945	0.03		

^aEpistatic interactions between two markers. In the case when the D allele at marker CFM6' (GL6) is associated with one allele from Z at marker CFF16 and when the peach allele at marker CFM6' is associated with the other allele from Z at marker CFF16, fruit mass is enhanced in comparison with the two other possible associations of alleles

^bEpistatic interactions between two markers. In this case, the only association favorable to stone mass is that between the peach allele at marker AG108 (GL5) and one of the two alleles from S at marker CFF6

can be explained by the fact there were fewer observed individuals in 2001. Indeed, the fraction of total variations in each trait explained by the QTLs was generally smaller in 2001 than in 2002. Moreover, in 2001 non-limiting fruit growth conditions (i.e., potential growth) were hardly attained for all genotypes. Accordingly, the different conditions of growth between years may have affected differently the various traits studied. However, this poor stability between putative QTL loci between years is in

agreement with the literature results. Indeed, few QTLs were identified for fruit quality traits (Etienne et al. 2002) and few QTLs were identified as stable through various years for different fruit quality traits. Dirlewanger et al. (1999) identified one QTL stable over 2 years for fresh weight and sorbitol concentration and two QTLs for maturity date, malic and citric acid concentrations. Similarly, Verde et al. (2002) identified only one or two

QTLs stable over years for blooming and maturity dates, fruit skin color and soluble solid content.

Traits with positive horticultural effects provided by D

As expected, D was found to provide favorable alleles for fruit traits which were therefore often opposite to the D phenotype. These QTLs appeared to be reliable because they were often detected in both years or explained a fairly high percentage of the total variation of the trait.

Several alleles provided by D appeared to increase the four individual sugar concentrations, despite the low sugar concentrations observed in D fruits (Moing et al. 2003). Alleles from D elevated sucrose (LG3), glucose (LG2, LG4, LG5 and LG7) and sorbitol (LG2) concentrations. Remarkably, in all QTLs for glucose concentration (on LG2, LG4, LG5 and LG7), D alleles were associated with an elevation in the glucose concentration. Except at the FRU locus, D alleles at QTLs controlling the fructose concentration (on LG2, 4 and 7) also caused an elevation in levels. This should be positive in terms of fruit sweetness, since fructose is sweeter than the three other individual sugars (Pangborn 1963).

The increasing effect of D alleles (found on LG1 and LG3) was expected for malic acid concentrations, since D fruits were shown to contain higher malic acid concentrations than cultivars (Moing et al. 2003), but this did not apply for citric acid concentrations which reached only very low levels in D fruits.

Surprisingly, favorable D alleles were found for fruit size, even though this was clearly opposite to the D phenotype. D provided three alleles (LG1 and LG4) that decreased stone size (mass and diameter).

Two alleles (LG1 and LG3) from D were found to increase red flesh coloration, although no red coloration could be observed on D fruits, which were all greenish yellow.

Unfavorable traits provided by D

As expected from the D phenotype and the distribution of quality trait levels in the population, D was also found to provide unfavorable alleles for several fruit traits. Three main regions of the genome harbored QTLs for several quality traits with unfavorable effects associated to the D allele. They were located near FRU (LG1), G (LG5) and PC60. In the region near FRU, D alleles were associated with smaller fruit size (at a QTL accounting for 12% of phenotypic variation), in addition to low fructose concentrations (46–55%) and sweetness (21%). On a narrow region of LG5 harboring the morphological marker G, alleles from D negatively affected skin coloration, fruit size (accounting respectively for 29 and 6% of phenotypic variation) and various gustative traits. As for the third region, on LG6, D alleles affected stone size (41% of stone diameter variations). Elimination of these regions should

not have any major adverse effects on other traits since no favorable D alleles were found in these regions.

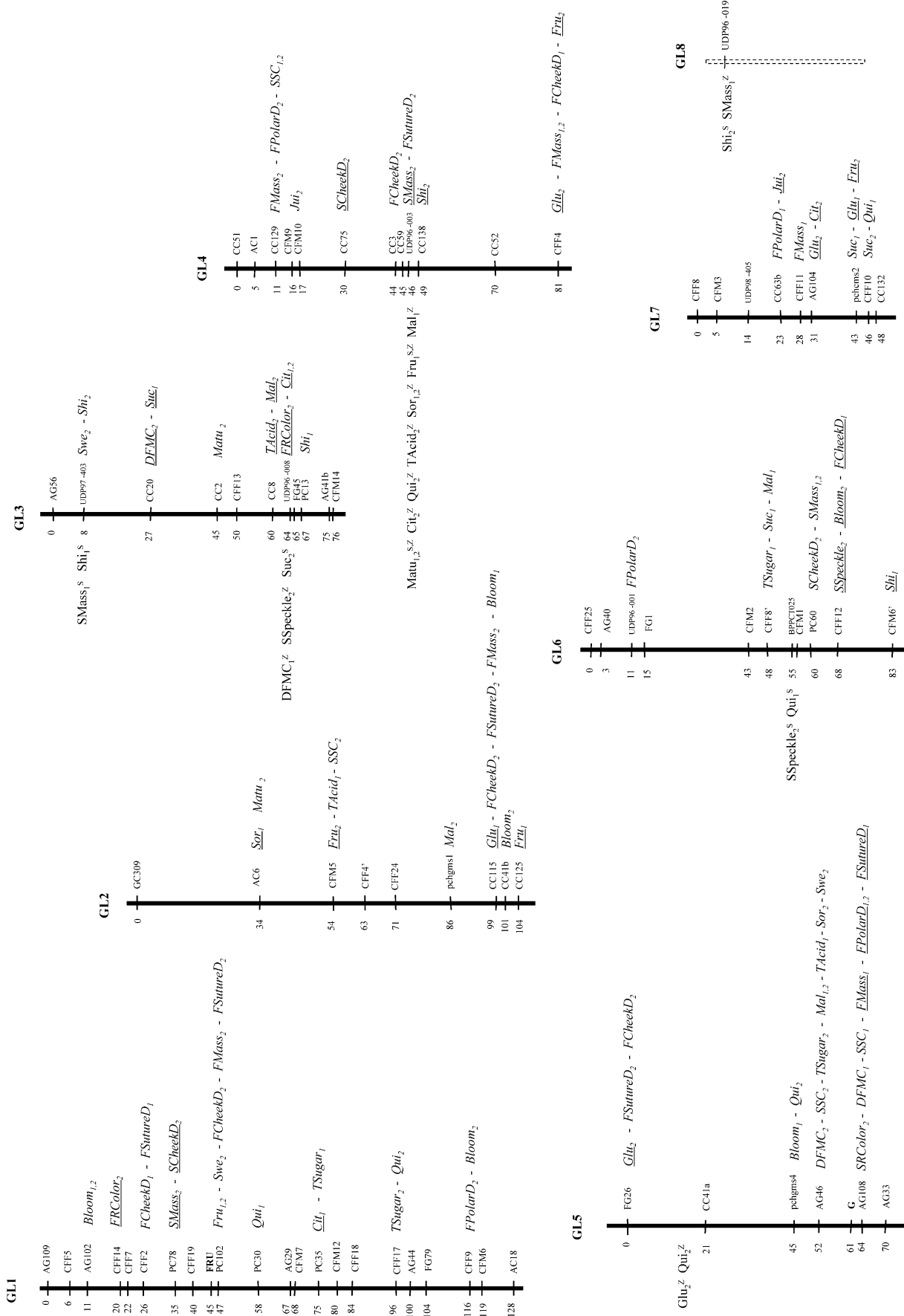
Co-location of QTLs for fruit quality and resistance to powdery mildew

In terms of breeding, it is interesting to identify co-locations between QTLs, especially when their effects have opposing horticultural results. At QTLs controlling stone and fruit size (mass and/or dimensions), D alleles similarly affected fruit and stone traits, reducing both on LG1 and LG4 and increasing both on LG6. They therefore had opposite effects on those two traits from a horticultural perspective, where the goal is to obtain big fruits with small stones. As for individual sugar concentrations, the QTLs detected on LG7 that increased glucose and fructose concentrations also decreased sucrose concentrations, in line with the comparisons of sugar concentrations and the hexose-to-sucrose ratio in D and commercial hybrid fruits. Favorable alleles from D, increasing glucose and fructose concentrations, were often co-located with alleles reducing fruit size (LG4 and LG5). Thus, suppressing the region near CFF4 (LG4) in order to eliminate alleles arising from D which reduce fruit mass will result in eliminating alleles which also increase glucose and fructose concentrations.

Considering the breeding objectives of the population studied, we also searched for co-locations between QTLs for quality traits and resistance factors to powdery mildew (Foulongne et al. 2003). Several co-locations were observed between QTLs for powdery mildew resistance and for quality traits. A QTL for powdery mildew resistance was detected in the same region as the major QTL for stone cheek diameter in this BC₂ population (Foulongne et al. 2003) on LG6. Thus, suppression of the D allele causing thick stones might be troublesome. On LG4, two QTLs with favorable effects of D alleles on powdery mildew resistance were detected (Foulongne et al. 2003) in two regions where D alleles reduced fruit size and stone size, respectively. In this case, the correlation between stone size and resistance was favorable from a breeding point of view. On LG5, QTLs for powdery mildew resistance were detected by Foulongne et al. (2003) on the same regions as QTLs with unfavorable effects of D alleles for fruit composition and dimension traits.

Possible physiological mechanisms underlying QTL co-locations

Co-located QTLs either correspond to distinct, closely linked genes or to a unique gene with a pleiotropic effect on several traits influenced by the same physiological process. Knowledge of the processes involved in fruit development and growth and in the resistance to or defense against pests and diseases provides some indications as to the likelihood of pleiotropic effects.



◀ **Fig. 2** Location of putative QTLs controlling fruit quality traits analyzed for two successive years: blooming date (*Bloom*), fruit polar diameter (*FPolarD*), fruit cheek diameter (*FCheekD*), fruit suture diameter (*FSutureD*), stone cheek diameter (*SCheekD*), fresh fruit mass (*FMass*), fresh stone mass (*SMass*), dry flesh mass content (*DFMC*), soluble solid content (*SSC*), sucrose (*Suc*), glucose (*Glu*), fructose (*Fru*), sorbitol (*Sor*), total sugar (*TSugar*) concentrations, malic acid (*Mal*), citric acid (*Cit*), quinic acid (*Qui*), shikimic acid (*Shi*), total acid (*TAcid*) concentrations, red skin coloration (*SRColor*), skin speckle (*SSpeckle*), red flesh coloration (*FRColor*), juiciness (*Jui*) and sweetness (*Swe*). Markers are listed to the right of each linkage group and genetic distances on the left. QTLs associated with markers of S or Z (*superscript*) genomes that could be assigned to linkage groups are listed to the left of each linkage group. QTLs associated with markers of the D genome are listed in *italics* to the right of each linkage group. *Underlined* QTLs are those for which the D allele confers a positive horticultural effect. The year of observation is denoted by 1 and 2 for 2001 and 2002, respectively. When co-located, QTLs are ordered by decreasing individual contribution from left to right on each side of the linkage group

Quantitative trait loci for sugar and acid traits were associated with maturity date and linked to UDP96-003, the marker for the Z genome on LG4. The reduction of citric, quinic and total acid concentrations and the elevation of sorbitol and malic acid concentrations were associated with an extension of growth duration. Citric and quinic acid concentrations were shown to decline (Liverani and Cangini 1991; Chapman and Horvat 1990) and malic acid levels to rise at the very end of fruit development (Wang et al. 1993; Moing et al. 1998). This suggests that fruits of early-maturing genotypes would not complete their physiological maturation as thoroughly as fruits of late-maturing genotypes, which could be explained by the early fall of fruits independently of achieving physiological maturity. In the same way, the positive correlation between sorbitol concentrations and growth duration may be related to an increase in the sorbitol concentration during longer fruit maturation. However, an increase in the sucrose rather than the sorbitol concentration is generally observed with maturation (Génard et al. 2003).

Quantitative trait loci for fructose and glucose concentrations were often co-located. These co-locations probably correspond to a unique gene with a pleiotropic effect since in the peach, glucose and fructose are absent from the phloem sap (Moing et al. 1992) and are synthesized concurrently by sucrose and sorbitol hydrolysis. In the same way, the co-location of QTLs for sucrose and for the two hexoses on LG7, with opposite effects of the D allele, probably correspond to a unique QTL controlling the activity of an enzyme. Indeed, acid invertase and neutral invertase are involved in sucrose hydrolysis, and sucrose phosphate synthase, which is a reversible enzyme, is involved in sucrose synthesis from glucose and fructose (Keener et al. 1979; Yamaki and Asakura 1988). The study of co-locations between functional candidate genes and the QTLs controlling sugar and acid concentrations may help to further assess these hypotheses and their possible pleiotropic effects. The co-location of a QTL for sweetness near the major QTL for fructose concentrations undoubt-

edly results from a pleiotropic effect linked to high fructose sweetness.

Two ecophysiological processes may explain the co-locations of QTLs for fructose and glucose concentrations with QTLs having an opposite effect on fruit size (LG2, LG4, LG5 and LG7). First, a low fruit fresh mass may stem from less water in the flesh which thus contributes to an increase in the sugar concentration. Second, because the contribution of each individual sugar to the osmotic potential of the fruit is different, the water flux caused by osmotic potential resulting in fruit fresh mass may be influenced by sugar composition. Another hypothesis to explain co-locations of QTLs affecting sugars and fruit size lies in the potential role of sucrose-cleaving enzymes in sugar composition and source-sink regulation (Klann et al. 1996; Roitsch 1999) and in the control of cell differentiation and development (Sturm and Tang 1999), both of which influence the elaboration of fruit size. Co-locations of QTLs affecting sugars and resistance factors (LG6) are also conceivable because of the role of enzymes such as invertase in the regulation of defense responses (Roitsch 1999).

As for fruit dimensions and fresh mass, co-located QTLs may evidently correspond to a unique QTL acting on fruit size. In the case of regions affecting both fruit and stone dimension (or fresh mass) as on LG1 and LG4, the existence of a unique QTL can also be hypothesized. This QTL might influence the dimensions of either stone and flesh or stone only. In the latter case, variations in stone size (mass or dimensions) alone would explain variations in fruit size, and such QTLs would not be of horticultural value. This was probably not the case in our study, since QTLs for flesh mass were also detected in regions controlling both fruit mass and stone size (data not shown). From a practical point of view, it is advisable always to study both fruit and stone dimensions to detect whether QTLs for fruit dimensions are not QTLs for stone dimensions. For instance, Dirlewanger et al. (1999) and Etienne et al. (2002) studied fresh fruit mass but not stone size. In the light of our results, the QTL they detected for fresh fruit mass on LG6 might correspond to a QTL for stone size, since it is located in the same region as the major QTL we detected for stone cheek diameter and stone mass.

Potential value to crop improvement

Some of the genome regions harboring favorable D alleles could easily be used to improve certain quality traits without affecting other quality or resistance factors. On LG3, two groups of co-located alleles from D presented favorable effects only, and should be used to improve dry flesh matter content, sucrose, malic acid, citric acid and total acid concentrations and red flesh coloration without impairing other traits, with the exception of the shikimic acid concentration, which is the least important acid in the peach.

Conversely, in several regions co-locations between QTLs for powdery mildew resistance and quality traits were observed. In most cases, selection for D alleles to improve resistance against pests and diseases may result in maintaining low agronomic traits. Fine-mapping experiments appear to constitute an efficient means of dissecting regions with clusters of QTLs. Using this method, Causse et al. (2002) succeeded in identifying three different QTLs in a cluster; one controlling fruit firmness, another controlling sugar and soluble solids content and another controlling fruit weight. Since increased resistance is the prime objective of this breeding program, fine mapping should concentrate on those regions. Alternatively, other cultivated germplasms could be prospected to further improve fruit traits controlled in those regions.

Fruit pubescence is a major trait in the commercial classification of peach varieties. Both nectarine and peach types should be produced in a breeding program. In order to cope with the co-location of a gene controlling fruit pubescence and a D allele dramatically reducing red skin color, it may be necessary to introgress the allele for peach fruits from a commercial variety. Alternative solutions to improve red skin coloration may lie in the identification and introgression of other alleles which improve coloration and suppression of the unfavorable S allele.

Whether D alleles which increase glucose and fructose concentrations are worth introgressing despite their co-location with unfavorable alleles which either reduce the sucrose concentration or fruit mass should be explored. Firstly, what will be the effect on sweetness of improving glucose and fructose concentrations while reducing the sucrose concentration? The use of an ecophysiological model simulating fruit growth and sugar accumulation (Génard et al. 2003) may be useful to further investigate the potential interest of D alleles in the case of co-locations with fruit mass QTLs. Secondly, do these co-locations result from a single gene with a pleiotropic effect? And thirdly, is it possible to sufficiently improve sucrose concentration and fruit mass in another way, i.e. by introgressing other favorable alleles from other germplasm, in order to compensate for the unfavorable effects of D alleles in those regions?

Limitations to QTL detection due to a lack of markers for Z and S

The correlations between 2001 and 2002 observations for each trait provided an order of magnitude of trait heritability. Accordingly, the fraction of the total variation of a trait explained by QTL was expected to be at most equal to the corresponding correlation. In most cases, it was lower. The most obvious case was the maturity date for which the r^2 only reached 0.39 and 0.53 in 2001 and 2002, respectively, whereas the correlation between years was much higher (0.93). For this reason, we hypothesize that we did not detect all the polymorphisms arising from the S and Z genomes regarding the maturity date in particular and, to a lesser extent, quality traits, which in

turn may have reduced the power of detecting D alleles affecting those traits. To cope with these limitations, we need to integrate new markers for the S and Z genomes. Until now, the integration of new markers for commercial variety genomes in peach genetic maps has appeared to be limited by a lack of polymorphism in these varieties (Etienne et al. 2002). However, the recent development of SSR markers throughout the peach genome (Aranzana et al. 2003) or in targeted regions on LG1, LG5 and LG6, opens more promising prospects for the future.

The BC₂ germplasm presents some major defects for agronomic traits which are the principal criteria for commercial quality, such as fruit size and red skin coloration. However, this germplasm also displays broad variations in many traits, and transgressive segregants are observed. The unexpected expression of some favorable alleles arising from wild species seems only to be efficient in an improved genetic germplasm. The QTL analysis we performed confirmed these potentialities, particularly regarding sugar concentrations. Our results suggested that some regions of the BC₂ genome have no effect on the traits studied. On the contrary, a few regions presented QTLs with a strong impact on quality traits, which could be either positive or negative. Finally, many regions harbored co-locations of QTLs for quality traits and resistance factors with opposite effects from a horticultural standpoint. In this case, the pursuit of fine mapping may be one efficient solution. For this reason, it does not appear useful in terms of improving quality to focus future efforts on suppressing a large percentage of the D genome. Furthermore, D may still harbor resistance factors which are as yet undetected. We propose initially to eliminate the three main regions of chromosome which appeared to be highly unfavourable. It would then seem worthwhile to focus on the fine mapping of the regions identified as harboring problematic co-locations.

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