Theor Appl Genet (1999) 98: 18–31

E. Dirlewanger · A. Moing · C. Rothan
L. Svanella · V. Pronier · A. Guye
C. Plomion · R. Monet

Mapping QTLs controlling fruit quality in peach (*Prunus persica* (L.) Batsch)

Received: 10 October 1997 /Accepted: 18 August 1998

Abstract The organoleptic quality of fleshy fruits is in a large part defined by their composition of soluble sugars and organic acids. An F_2 population issuing from a cross between two peach varieties, 'Ferjalou Jalousia', a non-acid peach, and 'Fantasia', an acid nectarine, was analysed over 2 successive years for agronomic characters and for molecular-marker (isoenzymes, RFLPs, RAPDs, IMAs and AFLPs) segregations. Blooming and maturity dates, as well as productivity, were noted for each tree. Four fruits per tree were analysed at maturity for fresh weight, colour, pH, titratable acidity, soluble-solids content (SSC), acid (malic, citric and quinic acids) and sugar (sucrose, glucose, fructose, sorbitol) contents. QTLs were detected for all fruit components analysed, except for fruit colour. The QTLs for nearly all components were present on two linkage groups. For productivity, fresh weight, pH, quinic acid, sucrose and sorbitol content, all the detected QTLs displayed the same effect as the parental phenotypes. By contrast, for maturity date, titratable acidity, malic and citric acids and fructose, some QTLs displayed the same effect as the parental phenotypes while others displayed the opposite effect. The fraction of the total variation in each trait throughout the population explained by the QTLs was very high and reached more than 90% for some characters. For most of the characters analysed, epistasis was observed between QTLs.

Key words Fruit quality · Organic acids · Sugars · Genetic linkage map · Quantitative trait loci (QTLs) · Peach (*Prunus persica*)

Communicated by M. A. Saghai Maroof

E. Dirlewanger (✉) · A. Moing · L. Svanella · V. Pronier
A. Guye · R. Monet
INRA, Unité de Recherche sur les Espèces Fruitières et la Vigne, Centre de Bordeaux, BP 81, 33883 Villenave d'Ornon cedex, France
Fax: + 335 56 84 30 83

C. Rothan
INRA, Station de Physiologie Végétale, Centre de Bordeaux, BP 81, 33883 Villenave d'Ornon cedex, France

C. Plomion
INRA, Laboratoire de Génétique et Amélioration des Arbres Forestiers, BP45, F-33610 Cestas, France

Introduction

Fruit producers must satisfy consumers by producing fruits of good flavour, colour and texture and must also provide marketers with fruits resistant to mechanical damage. In peach production, where the turnover of new cultivars is very rapid, size, firmness and appearance have now been improved through selection and have now reached an excellent level. On the other hand, flavour maintenance or improvement has been much slower to respond because this character is complex and difficult to control. The biological and genetic bases of fruit quality are still poorly known (Tucker 1993). The variation in fruit quality at harvest is related to a large number of interrelated factors (Génard and Bruchou 1992). However, acid and sugar content and composition are major determinants of peach quality. The sugar-acid ratio is thus commonly used as a quality index (Robertson et al. 1989; Bassi and Selli 1990). Three organic acids are predominant in peach fruit: malic, citric and quinic (Byrne et al. 1991). Malic acid is the most abundant at maturity (50–60% of total organic acids), citric (20–25%) and quinic (20–25%) being present in lower quantities. The soluble sugars present in peach are sucrose, fructose, glucose and sorbitol. Sucrose is the predominant soluble sugar at maturity (54–75% of total soluble carbohydrates) while sorbitol accumulates at very low levels (4–11%). Glucose (9–21%) and fructose (3–25%) reach similar levels (Yoshida 1970; Meredith et al. 1989; Bassi and Selli 1990).

The fruits with a 'non-acid' character are characterised at maturity by a pH higher than 4.0, a titratable

acidity lower than 40 milli-equivalents per litre and a soluble-solids content in the same range of magnitude as 'acid' fruits (Yoshida 1970; Monet 1979). The malic acid content in some 'non-acid' fruit varieties seems to be low (Byrne et al. 1991; Moing et al. 1997) and the hypothesis that, contrary to other fruits, this acid is not accumulated in the 'non-acid' fruit at maturity has been suggested by Monet (1979). The determinism of this character was reported to be controlled by a single dominant gene *D* (Yoshiba 1970; Monet 1979). This gene was located on a genetic linkage map constructed by using the progeny of a cross between two peach varieties, one with 'non-acid' fruit and the other with normal 'acid' fruit (Dirlewanger et al. 1998). The map covers 712 cM and includes 249 markers: involving four agronomic characters [male sterility (*ps*), flat (S-) or round fruit (ss), peach (G-) or nectarine (gg) and 'non-acid' (D-) or 'normal' fruit (dd)], one isoenzyme, 47 RFLPs, 82 RAPDs, six IMAs and 109 AFLPs. According to the previous estimated size of the peach genome, between 550 and 740 cM (Dirlewanger et al. 1996), which is in agreement with a previous map (Foolad et al. 1995), this map covers almost the entire genome.

The reduction of fruit quality into a number of elementary components has a practical objective, i.e. the marker-assisted selection of fruit with desirable taste characteristics, and a fundamental objective, which is an understanding of the molecular bases of quality. In some other fruits, particularly in tomato, QTLs controlling soluble-solids content have already been detected (Osborn et al. 1987; Paterson et al. 1988; Tanksley and Hewitt 1988; Garvey and Hewitt 1992), but as yet no similar approach has been reported for peach fruit. Moreover, in most of the published work related to QTLs, their location is still imprecise and their functional role remains unknown. When genes of known function are cloned, possible effects of their polymorphism on the variability of certain phenotypic traits can be examined. The 'candidate gene' strategy has been successfully used in maize for detecting genes controlling grain starch and protein content (Edwards et al. 1992), carbon-enzyme activities and carbohydrate concentration involved in early growth variability (Causse et al. 1995).

The aim of the present study was to identify QTLs for the major components of fruit quality in peach, by measuring several tree characters possibly interfering with fruit quality, such as blooming date, fruit maturity date and the fruit main sugar and organic-acid contents. Furthermore, we tried to identify genes controlling the above mentioned agronomic characters using a candidate gene approach.

Materials and methods

Population development

In 1988, 'Ferjalou Jalousia', a peach variety producing 'non-acid' flat fruit, was pollinated with pollen from 'Fantasia', an acid nectarine. In 1992, a hybrid with low-acidity fruits was self-pollinated, producing an F_2 population of 63 trees. The seedlings were germinated in vitro, transferred to the greenhouse and transplanted in the orchard in 1993. 'Ferjalou Jalousia', 'Fantasia' and the F_1 parent of the F_2 offspring were grafted onto 'Rubira' rootstock. 'Ferjalou Jalousia' and 'Fantasia' were cultivated outdoors in containers. The F_1 parent was transplanted to the orchard near the F_2 offspring in 1993. The trees were grown in a rich sandy loam soil, under a typical oceanic climate, 45 km South of Bordeaux (45°N). An open-vase training system with light winter pruning and a $5\,m \times 2\,m$ spacing was adopted. Hand thinning was carried out to reduce fruit load on the heavily loaded trees. Pest control was performed as usual for peach. The F_2 trees and the grafted F_1 parent were analysed, when they were 3 and 4 years old (in 1995 and 1996), for several tree and fruit agronomic characters. The fruit characteristics at maturity of the parents and of the F_1 individual which was self-pollinated to produce the F_2 population, measured in 1995, are summarised in Table 1. The maturity for each tree was determined according to the softning of flesh. For 'Ferjalou Jalousia', 'Fantasia' and for the F_1 individual, the pH was 4.9, 3.6 and 4.5, respectively. Acid concentrations were much higher in 'Fantasia' than in 'Ferjalou Jalousia'. By contrast, sugar concentrations in 'Ferjalou Jalousia' were slightly higher than in 'Fantasia'.

Table 1 Fruit characteristics of 'Ferjalou Jalousia' and 'Fantasia' at maturity, and of the F_1 individual which was self-pollinated to give the F_2 population measured in 1995. Mean ± standard deviation of four fruits. Fresh weight corresponds to the entire fruit. The other measurements were made on fruit juice

Traits	'Ferjalou Jalousia'	'Fantasia'	F_1
Fresh weight (g)	111.5 ± 8.8	199.5 ± 8.8	136.7 ± 17.8
pH	4.9 ± 0.1	3.6 ± 0.04	4.5 ± 0.1
Titratable acidity (mEq/l)	27.5 ± 2.5	148.1 ± 16.0	40.0 ± 3.1
Soluble-solids content (%)	15.6 ± 0.7	15.8 ± 0.4	12.2 ± 0.4
Malic acid (g/l)	2.4 ± 0.4	6.9 ± 0.4	2.2 ± 0.2
Citric acid (g/l)	0.4 ± 0.1	2.9 ± 0.4	0.6 ± 0.1
Quinic acid (g/l)	1.2 ± 0.2	2.1 ± 0.2	1.1 ± 0.2
Sucrose (g/l)	81.3 ± 6.2	59.2 ± 5.6	72.9 ± 2.5
Glucose (g/l)	11.2 ± 1.2	12.6 ± 1.8	4.9 ± 0.4
Fructose (g/l)	8.4 ± 1.2	10.2 ± 1.5	7.0 ± 0.3
Sorbitol (g/l)	1.3 ± 0.4	2.8 ± 1.2	0.7 ± 0.3

Genotyping

For each F_2 tree, the agronomic characters segregating as simple characters were noted, i.e. male sterility, flat and round fruit, peach or nectarine and 'non acid' or 'normal' fruit (Dirlewanger et al. 1998). For the last character, although no formal taste analysis by a panel was performed, the acidity of the fruit was roughly estimated on one fruit per tree by one person.

For molecular-marker analyses, isoenzymes, RFLPs, RAPDs and AFLPs were employed to elaborate the linkage maps (Dirlewanger et al. 1998). The different molecular marker procedures are described in Dirlewanger et al. (1998). Several probe sources were used for RFLP analyses: genomic or cDNA probes of several *Prunus* species (*P. persica*, *P. amygdalus*, *P. avium*, *P. ferganensis*) as well as probes corresponding to genes putatively involved in the control of peach fruit development and composition in terms of sugars and acids. The latter were obtained from a differential screening of a peach fruit cDNA library between two early growth development stages of the 'Fantasia' variety (probes named PC) (Rothan et al. 1997). We sequenced some of them and located them on the genetic linkage map [(e.g. the phosphoenolpyruvate carboxylase (*PEPc*) candidate

gene for organic acid content, involved in the synthesis of the major organic acids (Blanke and Lentz 1989), a S28 ribosomal protein (S28) and a gene homologous to a tagged sequence of rice (EST-rice)]. The details of the map construction are described in Dirlewanger et al. (1998).

Quantitative characters

Quantitative characters were measured for 2 successive years, in 1995 and 1996, with the exception of fruit colour which was measured only in the 2nd year. The blooming date, when all the flowers are open, the maturity date, corresponding to the beginning of flesh softening, and the tree productivity were all noted. For productivity, trees were given a score ranging from 0 (no or very few fruits on the tree) to 5 (large number of fruits). For all the fruit characteristics, four fruits per tree were analysed separately. Skin colour and fresh weight were measured only at maturity. Skin colour was evaluated by dividing the surface area of the fruit into ten regions: 0 was given to the yellow regions and 1 to the red regions. The pH and titratable acidity were measured in fruit juice extracted with a hand press and centrifuged at 700 g for 10 min. The supernatant was used crude for pH measurement with a pH electrode, and diluted with de-ionized water for titration to an end pH of 8.3 with 0.1 N NaOH. The soluble-solid content (SSC) of the juice was determined with a hand refractometer. Five-hundred microliters of juice were rapidly fixed with ethanol at 80°C (ethanol : juice, 80 : 20, v/v) for further metabolite analysis. Organic-acid and sugar contents were measured in the fruit juice using HPLC. Soluble sugars were purified and analysed by HPLC with refractive-index detection, as described by Moing et al. (1992). Organic acids were analysed without purification, using anion exchange HPLC (IonPac AS-11 4 mm column and ATC pre-column from Dionex Corporation, Sunnywale Calif., USA). Elution was done with de-gassed NaOH solutions containing 16% (v/v) methanol with a 2 ml min^{-1} flow and according to the following gradient: 0 to 5 min, 0.5 to 4.2 mM NaOH; 5 to 15 min, 4.2 to 37.5 mM NaOH; and 17 min, 37.5 mM NaOH. Acid detection was carried out using a PED2 conductivity detector from the Dionex Corporation after anion chemical suppression with H_2SO_4. Sugar and organic-acid quantification were done with Millenium software from Waters (Milford Mass., USA) using standards from Sigma (St Louis Mo., USA).

Statistical analysis

A two-way analysis of variance was employed to test the significance of the effects due to genotype, year and their interaction. It was performed with the 'GLM' procedure of Statistical Analysis System software (SAS Institute Inc., Cary, N.C., USA). Correlations between characters were calculated using the 'CORR' procedure of SAS. The Spearman coefficient was also calculated. QTL analyses were performed using Mapmaker/QTL 1.1 (Lincoln et al. 1992a, b) and QGENE 2.23,5/96 (Nelson 1997**).** In order to clarify if MAPMAKER/QTL 1.1 can be used with data including dominant and co-dominant markers, three sets of data were analysed: (1) one set included co-dominant markers and dominant markers well dispersed throughout the map, (2) another set included only the co-dominant markers; with this set of data the map was only partially represented, and (3) the last set included the previous co-dominant markers and some additional ones resulting from the re-coding of trans-dominant linked marker (TDLM) pairs (trans referring to the repulsion linkage phase) as a "co-dominant megalocus", as recommend by Plomion et al. (1996). A threshold LOD score value of 2.5 was chosen for declaring the existence of a QTL. However, when a QTL was detected for a character in one year with a LOD > 2.5 and in the other year with a $2 <$ LOD < 2.5 in the same region, the latter was taken into account. The ratio of dominance (d) to additivity (a) was used to determine the mode of gene action based on the criteria of Stuber et al. (1987): $d/a = 0$–0.20, additive (A); $d/a = 0.20$–0.80, partial dominance (PD), $d/a = 0.80$–1.20, dominance (D); $d/a > 1.20$, overdominance (OD). The interactions between QTLs were tested with QGENE 2.23,5/96 using only the markers of the third set of data.

Results and discussion

Phenotypic distribution and correlation between characters

No significant difference between years ($P > 0.05$) was observed for titratable acidity, malic acid and glucose content (Table 2). On the other hand, significant mean differences ($P < 0.05$) were observed for all the other characters. In 1996, F_2 fruits presented a lower mean fresh weight, a lower pH and soluble-solids content, less quinic acid and sorbitol and more citric acid, sucrose and fructose. In peach fruit, a year effect has been reported for SSC, citric acid, fructose and sorbitol (Brooks et al. 1993). Due to highly significant genotype × year interactions for all traits, the data from 1995 and 1996 were analysed separately.

As previously reported, malic acid was the predominant organic acid (Table 2). Citric- and quinic-acid contents were about three-times lower, citric-acid content being slightly higher than that of quinic acid. Among sugars, sucrose presented the highest concentration and sorbitol the lowest one (Table 2). The glucose content of fruit was not significantly different between the 2 years, in contrast with fructose whose content was respectively lower and higher than those of glucose in 1995 and 1996.

The distributions of the different characters were very similar for the 2 years. Therefore, only those obtained in 1995 are shown in Figs. 1 and 2. For blooming and maturity dates, zero corresponds to the earliest tree of the F_2 progeny (19 March for blooming date and 29 June for maturity date). Several characters present

Table 2 Mean values of the F_2 individuals for the fruit characters measured in 1995 and 1996

Traits	Year		Year effect prob < F
	1995	1996	
Fresh weight (g)	138.0	111.1	0.0001
pH	4.13	3.88	0.0001
Titratable acidity (mEq/l)	72.3	74.1	0.6401
Soluble-solids content (%)	12.2	10.7	0.0001
Malic acid (g/l)	3.77	3.61	0.3696
Citric acid (g/l)	1.40	1.67	0.0094
Quinic acid (g/l)	1.28	1.09	0.0001
Sucrose (g/l)	64.6	71.1	0.0003
Glucose (g/l)	10.1	10.3	0.5395
Fructose (g/l)	8.6	13.0	0.0001
Sorbitol (g/l)	1.39	1.02	0.0019

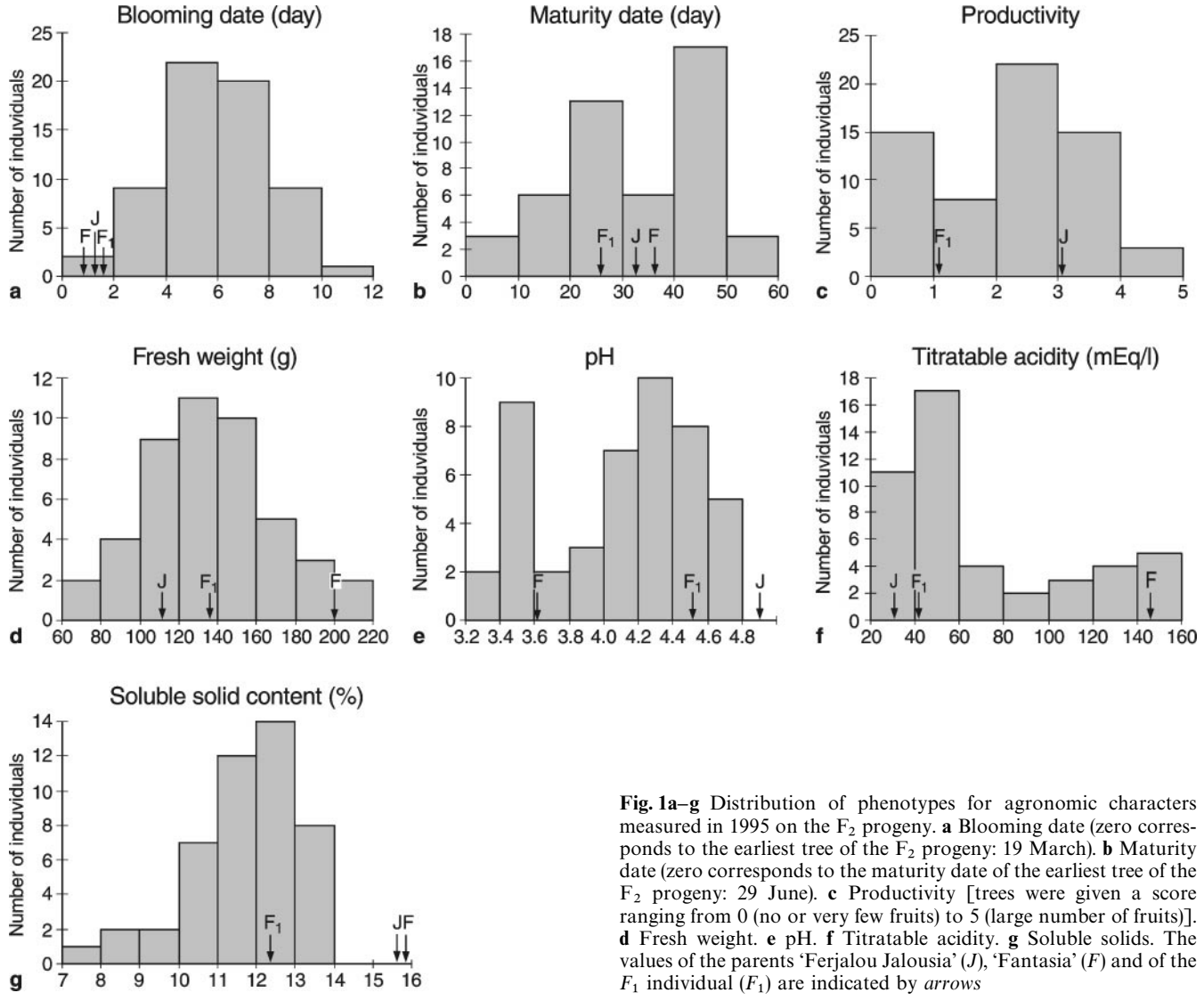


Fig. 1a–g Distribution of phenotypes for agronomic characters measured in 1995 on the F_2 progeny. **a** Blooming date (zero corresponds to the earliest tree of the F_2 progeny: 19 March). **b** Maturity date (zero corresponds to the maturity date of the earliest tree of the F_2 progeny: 29 June). **c** Productivity [trees were given a score ranging from 0 (no or very few fruits) to 5 (large number of fruits)]. **d** Fresh weight. **e** pH. **f** Titratable acidity. **g** Soluble solids. The values of the parents 'Ferjalou Jalousia' (*J*), 'Fantasia' (*F*) and of the F_1 individual (F_1) are indicated by *arrows*

a typical normal distribution, i.e. blooming date (Fig. 1 a), fresh fruit weight (Fig. 1 d), quinic acid (Fig. 2 c), sucrose (Fig. 2 d) and glucose (Fig. 2 e) contents. For pH (Fig. 1 e), titratable acidity (Fig. 1 f), malic- (Fig. 2 a) and citric-acid (Fig. 2b) contents, a bimodal distribution was observed. For pH, this result is in agreement with the segregation of the 'non-acid' fruit character: 1/4 with pH < 4 for acid fruits and 3/4 with pH > 4 for 'non-acid' fruits.

The Spearman correlation coefficients between traits are shown in Table 3. Blooming date was significantly negatively correlated with malic-acid content ($r = -0.29$, $P < 0.05$ in 1995): early blooming trees have fruits containing more malic acid. Maturity date was positively correlated with fresh weight ($r = 0.32$, $P < 0.05$ in 1995), titratable acidity ($r = 0.29$, $P < 0.05$ in 1995), SSC ($r = 0.39$, $P < 0.01$ in 1995) and fruit sugar contents [sucrose ($r = 0.35$, $P < 0.05$ in 1996), glucose ($r = 0.68$, $P < 0.01$ in 1996), fructose ($r = 0.48$ in 1995 and $r = 0.73$ in 1996 with $P < 0.01$) and sorbitol ($r = 0.47$ in 1995 and 0.63 in 1996 with $P < 0.01$)]. Fruit colour was significantly correlated with all characters. Titratable acidity and pH were highly negatively correlated. As previously suspected, pH was negatively correlated with all the acid concentrations, except with quinic acid in 1996, but also with glucose, fructose and sorbitol contents. pH was positively correlated with sucrose content. Acid contents were positively correlated, especially malic- and citric-acid contents ($r = 0.70$ in 1995, $r = 0.61$ in 1996 with $P < 0.01$). Soluble solids content was highly correlated with sucrose concentration ($r = 0.60$ in 1995, $r = 0.73$ in 1996 with $P < 0.01$), because sucrose is the main component of soluble solids, and citric-acid content was negatively correlated with sucrose content ($r = -0.55$ in 1995, $r = -0.48$ in 1996 with $P < 0.01$). Similar results were

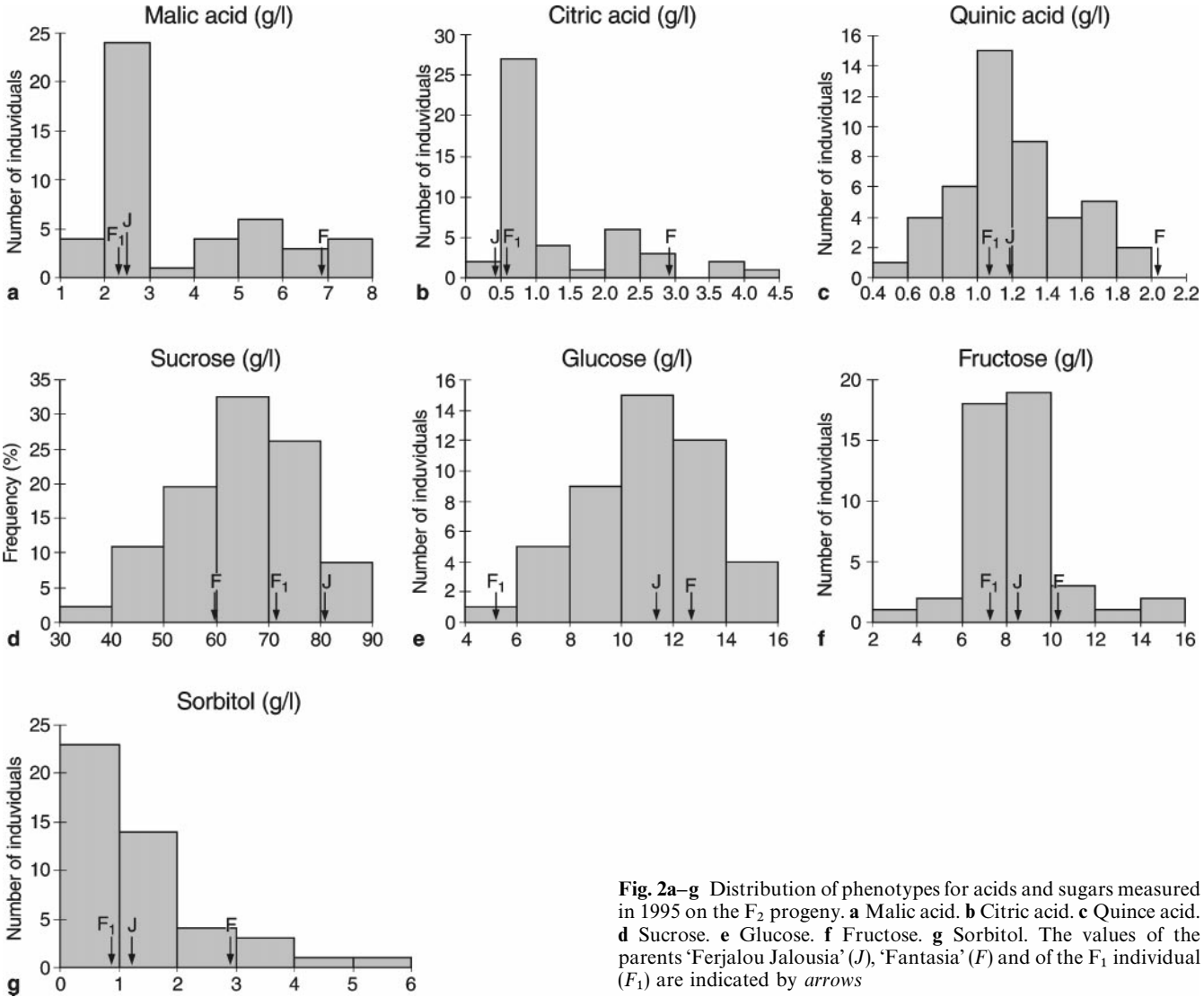


Fig. 2a–g Distribution of phenotypes for acids and sugars measured in 1995 on the F_2 progeny. **a** Malic acid. **b** Citric acid. **c** Quince acid. **d** Sucrose. **e** Glucose. **f** Fructose. **g** Sorbitol. The values of the parents 'Ferjalou Jalousia' (*J*), 'Fantasia' (*F*) and of the F_1 individual (F_1) are indicated by *arrows*

previously reported by Génard and Bruchou (1992). For sugars, the highest correlation was between glucose and fructose ($r = 0.78$ in 1995, $r = 0.90$ in 1996 with $P < 0.01$).

QTL detection

The results obtained with the first set of data including co-dominant and dominant markers well dispersed throughout the map are summarised in Table 4 and in Fig. 3. QTLs were detected for all the quantitative characters analysed, except for skin colour. With the second set of data, including only the co-dominant markers, all the QTLs previously detected within the region covered by these markers were detected again and their effects and positions were exactly the same as those calculated with the first set of data. With the third set of data, including co-dominant markers and TDLM pairs covering nearly all the map, the same results as for the first set of data were obtained. This suggests that MAPMAKER/QTL can be used with both dominant and co-dominant markers. This is due to the fact that QTL effects are calculated at the position of the LOD peak and not at the nearest marker.

The limited size of the F_2 implies that only QTLs with large effects could reach statistical significance (Andersson et al. 1994). For this reason, the number of QTLs found must be considered as a minimal estimate. The threshold we chose results from a compromise between preserving a sufficient power and limiting the risk of false-positives. On linkage groups 5 and 6, QTLs for nearly all characters were detected. Moreover, QTLs for several traits were detected in the same region. These may correspond to distinct closely linked QTLs or to only one QTL with a pleiotropic effect on

Table 3 Spearman correlation coefficients between traits measured on the tree or fruit in the F_2 progeny for two succesive years. For the fruit characteristics the correlation coefficients were calculated with four values per tree

Traits	Year	Blooming date	Maturity date	Productivity date	Fresh weight	Colour	pH	Titratable acidity	SSC	Malic acid	Citric acid	Quinic acid	Sucrose	Glucose	Fructose
Maturity date	1995	− 0.19													
	1996	− 0.03													
Productivity	1995	0.09	0.21												
	1996	0.29	− 0.04												
Fresh weight	1995	0.06	0.32*	0.44**											
	1996	0.02	− 0.16	− 0.19											
Colour	1995	–	–	–	–										
	1996	0.05	0.07	0.03	0.01										
pH	1995	0.04	− 0.15	− 0.16	− 0.11	–									
	1996	0.19	− 0.23	− 0.05	− 0.33**	− 0.09									
Titratable	1995	− 0.19	0.29*	0.09	0.06	–	− 0.89**								
acidity	1996	− 0.20	0.19	− 0.12	0.28**	− 0.01	− 0.83**								
SSC	1995	0.05	0.39**	− 0.34*	− 0.03	–	0.17*	− 0.05							
	1996	− 0.01	0.25	− 0.10	− 0.02	0.12	0.16*	− 0.22**							
Malic acid	1995	− 0.29*	0.14	0.02	0.06	–	− 0.75**	0.81**	− 0.09						
	1996	− 0.22	0.10	− 0.14	0.05	0.05	− 0.70**	0.73**	− 0.09						
Citric acid	1995	− 0.12	0.05	0.23	0.11	–	− 0.77**	0.79**	− 0.30**	0.70**					
	1996	− 0.20	− 0.05	− 0.07	0.33**	− 0.05	− 0.82**	0.81**	− 0.34**	0.61**					
Quinic acid	1995	− 0.09	− 0.08	− 0.36*	− 0.12	–	− 0.30**	0.27**	0.19**	0.32**	0.30**				
	1996	− 0.24	− 0.17	− 0.31*	0.15	− 0.11	− 0.03	0.05	0.24**	0.02	0.20**				
Sucrose	1995	0.12	− 0.14	− 0.32*	− 0.14	–	0.53**	− 0.49**	0.60**	− 0.39**	− 0.55**	− 0.05			
	1996	0.06	0.35*	0.04	− 0.11	0.02	0.30**	− 0.32**	0.73**	− 0.23**	− 0.48**	0.12			
Glucose	1995	0.12	0.23	0.05	0.05	–	− 0.30**	0.25**	0.37**	0.17*	0.18*	0.31**	0.24**		
	1996	− 0.14	0.68**	− 0.08	0.00	− 0.02	− 0.37**	0.30**	0.12	0.17*	0.24**	0.11	0.26**		
Fructose	1995	0.01	0.48**	0.16	0.13	–	− 0.54**	0.52**	0.26**	0.37**	0.34**	0.26**	− 0.06	0.78**	
	1996	− 0.20	0.73**	− 0.04	− 0.03	− 0.06	− 0.27**	0.22**	0.11	0.05	0.18*	0.14	0.25**	0.90**	
Sorbitol	1995	− 0.39	0.47**	− 0.19	0.12	–	− 0.34**	0.50**	0.43**	0.48**	0.26**	0.20**	0.08	0.37**	0.47**
	1996	− 0.15	0.63**	− 0.14	0.01	0.01	− 0.29**	0.26**	0.48**	0.30**	0.07	0.20**	0.53**	0.54**	0.50**

* $P < 0.05$; ** $P < 0.01$; Others not significant

Table 4 Linkage group locations, effects and modes of gene action of individual QTLs detected using Mapmaker/QTL with a minimum LOD score threshold of 2.5. LG = linkage group referring to the map, Dist = QTL position described by the distance (cM) from the 'top' of the linkage group. R^2 = fraction of the total variation explained by the QTL. a = additive effect expressed as the effect of substituting a 'Ferjalou Jalousia' allele (J) for a 'Fantasia' allele (F). d = dominance effect of the 'Ferjalou Jalousia' allele to a 'Fantasia' allele. d/a = ratio of the dominance to additive effects. The explanation for the mode of gene action of QTLs was given in the text. Direc. = the direction of additive effect on the phenotype

Trait	Year	LG		R^2	LOD	F/F	J/F	J/J	Gene action				
		Location	Dist						a	d	d/a	Mode	Direc.
Blooming date (100%)	1995	2	18	27.4	4.1	17.8	16.4	15.0	−1.4	0.0	0.0	A	F
	1996	7	10	20.5	3.0	22.2	23.0	24.4	1.1	−0.3	−0.3	PD	J
Maturity date	1995	3	0	24.3	2.8	41.9	34.5	21.6	−10.1	2.7	−0.3	PD	F
		4	2	61.7	8.6	17.3	32.2	45.9	14.3	0.6	0.0	A	J
		T		*64.6*	*9.4*								
	1996	3	0	21.3	2.3	46.1	41.6	29.6	−8.3	3.7	−0.4	PD	F
		4	2	60.3	7.5	26.5	37.5	51.5	12.5	−1.5	−0.1	A	J
		T		*66.5*	*8.2*								
Productivity	1995	6	91	76.0	18.8	2.9	2.0	0.1	−1.4	0.5	−0.3	PD	F
		9	13	62.3	2.6	2.1	2.4	0.3	−0.9	1.2	−1.3	OD	F
		T		*75.8*	*18.9*								
	1996	1	114	62.0	3.4	3.0	3.3	0.3	−1.4	1.7	−1.2	D	F
		6	90	72.9	17.8	3.4	3.4	0.4	−1.4	1.5	−1.1	D	F
		9	4	76.2	7.7	2.9	3.5	0.3	−1.3	1.9	−1.5	OD	F
		T		*75.6*	*18.3*								
Fresh weight	1995	6	95	47.8	5.2	166.9	153.5	100.9	−33.0	−20.5	0.6	PD	F
	1996	6	92	22.6	2.6	128.0	99.0	99.3	−14.4	−14.6	1.0	D	F
pH	1995	5	9	69.7	11.8	3.57	4.24	4.45	0.4	0.3	0.6	PD	J
		6	8	79.0	5.7	3.61	4.44	3.85	0.1	0.7	5.9	OD	J
		8	31	73.3	3.1	3.59	4.47	3.95	0.2	0.7	3.9	OD	J
		T		*86.8*	*15.7*								
	1996	5	9	52.6	7.7	3.40	4.02	4.19	0.4	0.2	0.6	PD	J
		6	6	68.5	3.8	3.50	4.23	3.64	0.1	0.7	9.4	OD	J
		T		*88.3*	*11.4*								
Titratable acidity	1995	1	106	85.6	6.1	58.5	47.0	129.3	35.4	−46.9	−1.3	OD	J
		5	8	87.0	17.3	129.0	50.4	47.0	−41.1	−37.6	0.9	D	F
		6	16	84.1	6.4	127.8	46.0	82.5	−21.3	−60.5	2.8	OD	F
		T		*99.2*	*28.15*								
	1996	1	108	73.9	3.2	62.7	55.4	124.1	30.7	−38.0	1.2	D	J
		5	8	78.5	10.0	124.8	59.9	51.2	−36.8	−28.1	0.8	PD	F
		6	8	81.6	7.0	120.6	51.5	102.2	−9.1	−59.9	6.5	OD	F
		T		*99.5*	*22.2*								

Table 4 Continued

Trait	Year	LG		R^2	LOD	F/F	J/F	J/J	Gene action				
		Location	Dist						a	d	d/a	Mode	Direc.
Soluble-solids content	1995	4	6	32.7	3.9	10.7	12.4	12.8	1.1	0.6	0.5	PD	J
	1996	6	94	35.7	3.7	9.8	11.3	9.6	−0.1	1.6	−16	OD	F
Malic acid	1995	1	106	74.7	4.2	3.45	2.62	6.57	1.6	−2.4	−1.5	OD	J
		5	32	78.0	12.1	6.47	2.86	2.57	−1.9	−1.7	0.8	PD	F
		6	7	78.6	5.4	6.02	3.28	5.50	−0.3	−3.3	12.8	OD	F
		T		*99.5*	*25.0*								
	1996	5	26	57.0	8.6	4.88	3.13	2.80	−1.0	−0.7	0.7	PD	F
		6	7	70.0	3.8	4.95	2.71	4.93	0.0	−2.2	—	OD	—
		T		*87.4*	*12.2*								
Citric acid	1995	5	9	81.7	14.0	2.82	0.84	0.86	−1.0	−1.0	1.0	D	F
		6	6	74.8	4.8	2.92	0.84	1.46	−0.7	−1.3	1.8	OD	F
		9	6	71.8	4.1	1.30	0.86	2.87	0.8	–1.3	–1.5	OD	J
		T		*96.1*	*17.2*								
	1996	5	9	57.6	8.7	2.84	1.36	1.10	−0.9	−0.6	0.7	PD	F
		6	9	68.8	3.7	2.71	1.09	1.77	−0.5	–1.1	2.4	OD	F
		T		*78.9*	*9.3*								
Quinic acid	1995	1	43	24.4	2.5	1.20	1.44	1.04	−0.1	0.3	4.0	OD	F
Sucrose	1995	5	9	34.2	4.2	53.2	68.0	68.0	7.3	8.1	1.1	D	J
	1996	5	43	25.5	2.8	59.9	77.7	79.3	8.1	9.7	1.2	D	J
		6	95	36.2	3.6	59.9	80.0	63.5	1.8	18.3	10.2	OD	J
		T		*50.2*	*6.0*								
Glucose	1996	8	3	29.5	3.3	12.00	11.50	8.10	−1.9	0.8	−0.4	PD	F
Fructose	1995	3	54	42.1	3.0	11.68	7.85	7.98	−1.9	−2.0	1.1	D	F
		4	11	25.1	2.8	6.69	8.78	9.49	1.5	0.6	0.4	PD	J
		5	37	26.0	2.9	10.23	8.05	7.51	−1.4	−0.8	0.6	PD	F
		T		*77.8*	*10.2*								
	1996	4	0	35.6	4.2	9.62	12.34	15.06	2.7	0.7	0.2	A	J
		8	6	36.5	4.5	15.70	13.64	9.88	−2.9	0.8	0.3	PD	F
		T		*85.7*	*11.9*								
Sorbitol	1995	1	108	62.9	3.3	0.96	1.18	4.32	1.7	−1.5	−0.9	D	J
		6	10	49.9	6.2	0.82	1.40	4.62	1.9	–1.3	−0.7	PD	J
		T		*83.5*	*10.6*								
	1996	6	4	69.7	2.6	1.92	0.62	1.81	0.0	−1.2	–	OD	–

Table 5 Interaction between markers located on distinct linkage groups detected using QGENEsoftware. Only pairs of markers with the highest *F* value of the two-way interaction are reported here. *F*-threshold for significance of single marker (one way ANOVA): 7.00, corresponding *P*-value for single test: 0.001852. *F*-threshold for significance of a two-way interaction:12, corresponding *P*-value for single test 1/1000

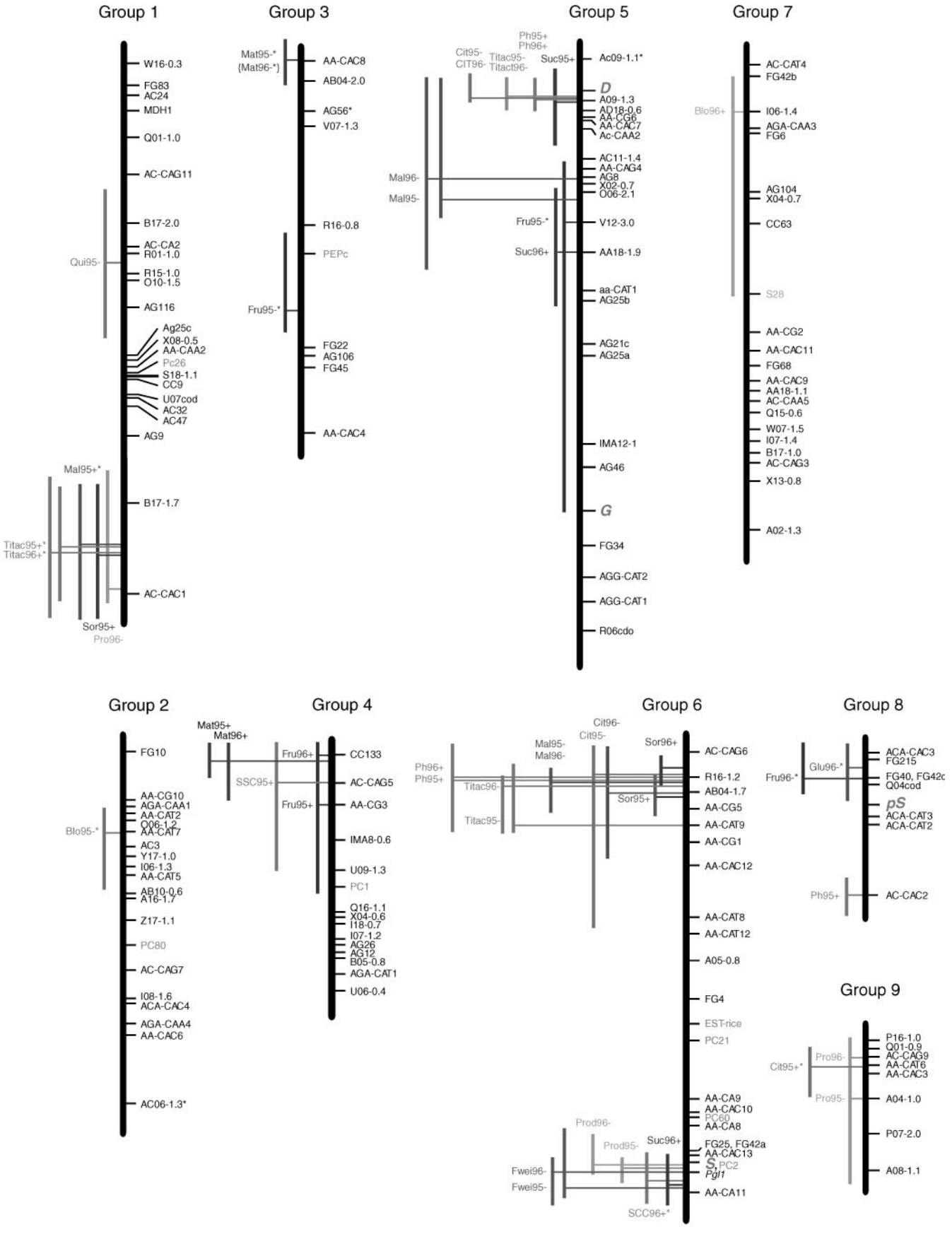
Trait	Year	Significant marker		Interaction			
		Marker	Group	Marker	Group	*F*	*P*
Blooming date	1995	AC31	2	AC47	1	39.52	0.00000
		„	„	AG56	3	77.63	0.00000
		„	„	AG21c	5	74.94	0.00000
		I6	2	2CC133	4	60.31	0.00000
Maturity date	1995	CC133	4	AG56	3	15.31	0.00033
		„	„	PC2	6	42.12	0.00000
		U9	4	S28	7	16.26	0.00027
	1996	CC133	4	AG56	3	30.03	0.00000
		„	„	PC2	6	36.18	0.00000
		„	„	FG42	7	19.00	0.00012
		PC1	4	AC9	5	14.65	0.00045
Productivity	1995	PC2	6	AC-CA2/R01-1.0	1	12.82	0.00069
	1996	PC2	6	AC-CA2/R01-1.0	1	18.06	0.00008
		„	„	O6	2	13.35	0.00056
		„	„	FG68	7	29.02	0.00000
		PC60	6	AA-CG6/AA-CAC7	5	13.08	0.00063
Fresh weight	1995	PC2	6	AC-CA2/R01-1.0	1	15.98	0.00025
		„	„	AA-CAC8/AB04-2.0	3	29.91	0.00000
		„	„	Q4cod	8	21;75	0.00003
		PGL1	6	AG12	4	21.24	0.00004
		„	„	FG34	5	13.03	0.00086
		„	„	FG42	7	24.23	0.00002
pH	1995	AC9	5	FG83	1	265.81	0.00000
		„	„	AG106	3	295.70	0.00000
		„	„	PC1	4	203.02	0.00000
		„	„	FG25	6	327.00	0.00000
		„	„	FG6	7	266.3	0.00000
		X2	5	I8	2	114.22	0.00000
	1996	AC9	5	FG83	1	126.85	0.00000
		„	„	AG106	3	169.76	0.00000
		„	„	PC1	4	124.08	0.00000
		„	„	PGL1	6	50.43	0.00000
		„	„	FG6	7	143.26	0.00000
		X2	5	I8	2	105.97	0.00000
Titratable acidity	1995	AC9	5	PC26	1	60.28	0.00000
		„	„	I6	2	15.78	0.00029
		„	„	AG56	3	23.71	0.00002
		„	„	PC1	4	77.29	0.00000
		„	„	PGL1	6	18.02	0.00000
		„	„	FG68	7	40.64	0.00000
	1996	AC9	5	AG9	1	14.19	0.00055
		„	„	PC1	4	15.79	0.00033
		„	„	FG68	7	18.53	0.00009
Soluble-solids content	1995	AC-CAG5/AA-CG3	4	AG56	3	102.72	0.00000
		„	„	PC2	6	284.69	0.00000
		PC1	4	AC9	5	38.72	0.00000
		„	„	FG42	7	37.56	0.00000
	1996	PC2	6	AC-CA2/R01-1.0	1	254.73	0.00000
		„	„	PC80	2	118.05	0.00000
		„	„	AA-CAC8/AB04-2.0	3	225.32	0.00000
		„	„	X04-0.6/I18-0.7	4	78.91	0.00000
		„	„	AG104	7	286.40	0.00000
		„	„	Q4cod	8	305.12	0.00000

Table 5 Continued

Trait	Year	Significant marker		Interaction			
		Marker	Group	Marker	Group	*F*	*P*
Malic acid	1995	AC9	5	PC26	1	53.80	0.00000
	„	„		AG56	3	21.77	0.00003
	„	„		X04–0.6/I18–0.7	4	24.02	0.00001
	„	„		FG68	7	30.97	0.00000
	1996	AA-CG6/AA-CAC7	5	AG9	1	15.81	0.00029
	„	„		AG56	3	38.02	0.00000
	„	„		FG25	6	17.59	0.00017
	AC9	5	PC1	4	13.10	0.00090	
Citric acid	1995	AC9	5	AC47	1	21.97	0.00004
	„	„		FG10	2	18.18	0.00011
	„	„		AG106	3	22.05	0.00003
	„	„		X4/I18	4	28.06	0.00000
	„	„		PGL1	6	16.54	0.00029
	„	„		AC-CAG3/X13-0.8	7	26.71	0.00001
	„	„		Q4cod	8	21.31	0.00004
	1996	AC9	5	AG12	4	15.94	0.00029
	„	„		FG68	7	20.51	0.00005
Sucrose	1995	AA-CG6/AA-CAC7	5	AC47	1	36.45	0.00000
	AC9	5	PC60	6	51.95	0.00000	
	„	„		FG68	7	36.53	0.00000
	1996	PC2	6	AC-CA2/R01-1.0	1	87.67	0.00000
	„	„		AA-CAC8/AB04-2.0	3	90.25	0.00000
	„	„		X4/I18	4	23.95	0.00000
	„	„		AG104	7	75.63	0.00000
	„	„		Q4cod	8	99.44	0.00000
Glucose	1996	FG40	8	FG22	3	21.58	0.00004
Fructose	1995	AC-CAG5/AA-CG3	4	AG56	3	25.27	0.00001
	„	„		PC2	6	40.40	0.00000
	1996	CC113	4	AG56	3	28.83	0.00000
	„	„		PC2	6	32.05	0.00000
	„	„		FG42	7	13.12	0.00097
	FG40	8	FG83	1	15.99	0.00029	
	„	„		FG22	3	32.46	0.00000
	„	„		ESTrice	6	12.42	0.00110
	FG215	8	R6cod	5	17.48	0.00014	
Sorbitol	1995	ESTrice	6	PC26	1	19.61	0.00007
	„	„		AC31	2	17.92	0.00012
	„	„		CC63	7	12.75	0.00094

a single gene acting upon several quantitative characters involved in the same metabolic pathway. This type of result has previously been observed on tomato chromosome 6 where the same QTL was apparently observed for fruit mass, pH and solid concentration (Paterson et al. 1988). The apparent co-location of QTLs for fruit pH and sugars found in tomato was also found in peach. A physiological interpretation for this situation has previously been reported (Prioul et al. 1997): a QTL for a proton-driven translocation of carbohydrate from the cytosol into the vacuole, or for the proton pump, is likely to affect both pH and soluble sugars. On linkage group 5, QTLs were located near the *D* gene controlling the 'non-acid' fruit character, including QTLs for pH and titratable acidity in agreement with the perception of acidity in the mouth. On linkage group 6 the two distal regions of the linkage group were involved in QTLs. Near the *S* gene, which is a dominant gene controlling fruit shape, i.e. flat or round (Lesley 1940), QTLs for fresh weight and productivity were detected. This is in agreement with the fact that flat fruits are generally lower in weight than round fruits. Moreover, evidence is given here that trees with flat fruit are less productive. QTLs controlling malic, citric acid and sorbitol contents were all located in the upper region of the linkage group.

For the pH of the juice, QTLs were detected on linkage group 5, as was expected, but also on linkage groups 6 and 8. The last one was detected only for the 1995 data. The QTLs on groups 5 and 6 presented exactly the same location in 1995 and 1996. They all produce effects in the same direction as the parental phenotypes: the 'Ferjalou Jalousia' alleles increased the pH of the juice. However, surprisingly, the QTL on linkage group 5 ($R^2 = 69.7$ in 1995 and 52.6 in 1996) had a lower effect than the QTL on linkage


Group 1
W16-0.3
FG83
AC24
MDH1
Q01-1.0
AC-CAG11
B17-2.0
Qui95-
AC-CA2
R01-1.0
R15-1.0
O10-1.5
AG116
Ag25c
X08-0.5
AA-CAA2
Pc26
S18-1.1
CC9
U07cod
AC32
AC47
AG9
Mal95+*
B17-1.7
Titac95+*
Titac96+*
AC-CAC1
Sor95+
Pro96-
Group 3
Mat95-*
{Mat96-*}
AA-CAC8
AB04-2.0
AG56*
V07-1.3
R16-0.8
PEPc
Fru95-*
FG22
AG106
FG45
AA-CAC4
Group 5
Ph95+
Ph96+
Cit95-
CIT96-
Titac95-
Titact96-
Suc95+
Ac09-1.1*
D
A09-1.3
AD18-0.6
AA-CG6
AA-CAC7
Ac-CAA2
AC11-1.4
AA-CAG4
AG8
Mal96-
X02-0.7
Mal95-
O06-2.1
Fru95-*
V12-3.0
Suc96+
AA18-1.9
aa-CAT1
AG25b
AG21c
AG25a
IMA12-1
AG46
G
FG34
AGG-CAT2
AGG-CAT1
R06cdo
Group 7
AC-CAT4
FG42b
Blo96+
I06-1.4
AGA-CAA3
FG6
AG104
X04-0.7
CC63
S28
AA-CG2
AA-CAC11
FG68
AA-CAC9
AA18-1.1
AC-CAA5
Q15-0.6
W07-1.5
I07-1.4
B17-1.0
AC-CAG3
X13-0.8
A02-1.3
Group 2
FG10
AA-CG10
AGA-CAA1
AA-CAT2
Q06-1.2
AA-CAT7
Blo95-*
AC3
Y17-1.0
I06-1.3
AA-CAT5
AB10-0.6
A16-1.7
Z17-1.1
PC80
AC-CAG7
I08-1.6
ACA-CAC4
AGA-CAA4
AA-CAC6
AC06-1.3*
Group 4
Mat95+
Mat96+
Fru96+
CC133
SSC95+
AC-CAG5
Fru95+
AA-CG3
IMA8-0.6
U09-1.3
PC1
Q16-1.1
X04-0.6
I18-0.7
I07-1.2
AG26
AG12
B05-0.8
AGA-CAT1
U06-0.4
Group 6
Cit96-
Cit95-
Mal95-
Mal96-
Sor96+
Ph96+
Ph95+
AC-CAG6
R16-1.2
Titac96-
AB04-1.7
Sor95+
AA-CG5
Titac95-
AA-CAT9
AA-CG1
AA-CAC12
AA-CAT8
AA-CAT12
A05-0.8
FG4
EST-rice
PC21
AA-CA9
AA-CAC10
PC60
AA-CA8
Prod96-
Prod95-
Suc96+
FG25, FG42a
AA-CAC13
S, PC2
Fwei96-
Pgl1
Fwei95-
AA-CA11
SCC96+*
Group 8
ACA-CAC3
FG215
Glu96-*
Fru96-*
FG40, FG42c
Q04cod
pS
ACA-CAT3
ACA-CAT2
Ph95+
AC-CAC2
Group 9
P16-1.0
Q01-0.9
Pro96-
AC-CAG9
Cit95+*
AA-CAT6
AA-CAC3
Pro95-
A04-1.0
P07-2.0
A08-1.1

group 6 ($R^2 = 79.0$ in 1995 and $R^2 = 68.5$ in 1996). The total variance of the character explained by the QTLs for pH was similar for each year, i.e. $R^2 = 86.8$ in 1995 and 88.3 in 1996. These results demonstrate that the pH of the juice presents a complex determinism with at least two major regions involved. In tomato, six QTLs for fruit pH were mapped and accounted for 48% of the phenotypic variance (Paterson et al. 1988).

For titratable acidity, three QTLs were detected on linkage groups 1, 5 and 6. Those on linkage groups 5 and 6 produced an effects in the same direction as the parental phenotypes: the 'Fantasia' alleles increased the titratable acidity of the fruit. They were located in the same region as the QTL detected for pH. The QTL on linkage group 1 produced an effect in the opposite direction. This provides a demonstration of transgression and indicates that some F_2 individuals or cultivars having alleles at the three QTLs producing effects in the same direction may exhibit more extreme phenotypes than the parental lines. The total variance of the character explained by the three QTLs was very high ($R^2 = 99.2$ in 1995 and 99.5 in 1996). For malic-acid concentration, similar results were obtained. QTLs on linkage groups 1, 5 and 6 were detected displaying the same effect as those for titratable acidity. For citric-acid concentration, QTLs were detected on linkage groups 5 and 6 but also on group 9. For pH, titratable acidity, malic and citric acids, each of the QTLs had a very pronounced effect. These results lead to several main conclusions which are applicable to other QTL analyses: (1) a small number of Mendelian factors can explain a large part of the genetic variance, and (2) traits for different characters frequently seem to share common QTLs.

For quinic acid and for sugars, an annual effect was observed, suggesting a high environmental influence on the expression of the character. The R^2 and LOD score values for these characters were much lower than for the others.

Interactions between markers were detected for many quantitative characters. The results obtained using QGENE software are summarised in Table 5. As the F_2 population was small (63 individuals) the effect of the interaction was not reported here because the estimation was not precise enough. For pH, exactly the same interactions were observed for both years. Markers on linkage group 5 interact with markers on all the other linkage groups except for group 8. Most of the interactions observed for pH were also observed for titratable acidity, malic and citric acids. The same markers (AC9), located on linkage group 5, interact with other markers located on several linkage groups for pH, titratable acidity, malic and citric acids and for sucrose concentration.

Fig. 3 Localisation of QTLs controlling fruit-quality components analysed for 2 successive years (1995 and 1996): blooming date (*Blo*), maturity date (*Mat*), tree productivity (*Pro*), fruit fresh weight (*Fwei*), pH, titratable acidity (*Titac*), soluble-solids content (*SSC*), malic (*Mal*), citric (*Cit*), quinic (*Qui*) acid contents and sucrose (*Suc*), glucose (*Glu*), fructose (*Fru*), sorbitol (*Sor*) contents. Only linkage groups including QTLs are represented. Loci are listed on the right of each linkage group. Not all of the markers located on the linkage map are indicated: for co-segregating markers only one was represented. Genes controlling agronomic characters or corresponding to candidate genes are indicated in *red*. Molecular markers presenting a deviation from the expected Mendelian ratio are noted with an *asterisk*. With respect to QTL localisation the highest probability is indicated by a *horizontal line* and the confidence interval by a *vertical line*. QTLs were detected using MAPMAKER/QTL. QTLs indicated in *brackets* present a $2.0 < \text{LOD} < 2.5$, for the others $\text{LOD} > 2.5$. The *sign* + or − indicates that the allele which increases the trait values is in the 'Ferjalou Jalousia' or in the 'Fantasia' parent respectively. The *asterisk* indicates that the QTL displays the opposite effect to the parental one

The candidate-gene approach

Eight putative candidate genes were located on the map: two with a known function [the PEPc (Group 3) the S28 ribosomal protein (Group 7)] and seven obtained from the differential screening of a peach fruit cDNA library at early growth stages: PC26 (Group 1), PC80 (Group 2), PC1 (Group 4), PC2, PC21, PC60 and ESTrice (Group 6) (Fig. 3). Only the PC2 clone was found close to the QTLs controlling fruit fresh weight, productivity, SSC and sucrose content. The PEPc was not located in the QTL region of any acid concentration. This suggests that this enzyme is not directly involved in the variation in acid content of the acid-less mutant analysed. One reason for this might be that PEPc is a highly regulated enzyme (Chollet et al. 1996). Other known genes involved in fruit sugar metabolism, such as sorbitol dehydrogenase and acid invertase (Yamaki and Ishikawa 1986; Moriguchi et al. 1990), or in the degradation of organic acids, such as malate dehydrogenase (Taureilles-Saurel et al. 1995) and malic enzyme (Ruffner et al. 1984), should be tested. Genes involved in the storage of organic acids in the vacuole, such as those responsible for tonoplastic H^+-ATPase and pyrophosphatase (Davies 1997), could also be valuable candidate genes. Unfortunately, the gene(s) responsible for tonoplastic malate transport through a malate transporter or a malate-selective anion channel remain(s) unknown (Cheffings et al. 1997).

Conclusion

The 'non-acid' character of peach fruit, as perceived in the mouth, is segregates like a monogenic dominant character, as previously reported (Yoshida 1970; Monet 1979). However, at least two QTLs for the pH of fruit juice, with similar high effects, were detected on different linkage groups for the 2 years of observation. These results indicate that the 'non-acid' fruit character is correlated with other characters besides the fruit pH. The perception of acidity in the mouth depends not only on the acid concentration but also on the type of

acid (Pangborn 1963). The concentration and type of sugars can also interfere with acid perception (Bassi and Selli 1990). It is therefore not surprising that QTLs were detected for citric and malic acids and for sucrose near the *D* gene controlling the 'non-acid' character. Consequently, to improve the fruit organoleptic quality, the QTLs associated with the different acid and sugar contents must be taken into account.

For productivity, fresh weight, pH, quinic acid, sucrose and sorbitol contents all the detected QTLs displayed effects in the same direction as the parental phenotypes. In contrast, for maturity date, titratable acidity, SSC, malic and citric acids, glucose and fructose, some QTLs displayed effects in both directions. For these characters it will be possible to select cultivars with higher values than the parent.

Except for fruit colour, QTLs for all the fruit components analysed were detected. Fruit colour was not correlated with any other character. A maximum of three QTLs was detected for each character. The fraction of the total variation in each trait throughout the population explained by QTLs was very high and reached more than 90% for some characters, suggesting that effective selection can occur with few markers.

On two linkage groups, QTLs for nearly all the components were present. This suggests that some QTLs may have a pleitropic effect. Some genes in this region could be involved in several metabolic pathways. Another hypothesis would be that these two regions include two cluster of genes involved in different pathways, as is frequently the case for disease resistance genes (Paran and Michelmore 1993; Ma et al. 1994).

Epistatic interactions between QTLs revealed a complex network, particularly between the genes controlling pH and titratable acidity. These results indicate that they act not only in an additive manner but also in interaction; for example, as limiting factors of a particular metabolic pathway.

Acknowledgements This work was supported by funds from the European Community in the context of the *Prunus* mapping project (AIR3-CT93-1585), INRA (AIP Génome des Plantes Cultivées and AIP 'AGRAF') and the Aquitaine Region program 'Détection de gènes d'intérêt écologique et économique chez les arbres forestiers et fruitiers'. We thank the "Les Jarres" INRA Experimental Station team in Toulenne for growing the plant material in their orchard.

References

Andersson L, Haley CS, Ellegren H (1994) Genetic mapping of quantitative trait loci for growth and fatness in pigs. Science 263:1771–1774

Bassi D, Selli R (1990) Evaluation of fruit quality in peach and apricot. Adv Hort Sci 4:107–112

Blanke MM, Lentz F (1989) Fruit photosynthesis. Plant Cell Environ 12:31–46

Brooks SJ, Moore JN, Murphy JB (1993) Quantitative and qualitative changes in sugar content of peach genotypes [*Prunus persica* (L.) Batsch]. J Am Soc Hort Sci 118:97–100

Byrne DH, Nikolic AN, Burns EE (1991) Variability in sugars, acids, firmness, and colour characteristics of 12 peach genotypes. J Am Soc Hort Sci 116:1004–1006

Causse M, Rocher JP, Henry AM, Charcosset A, Prioul JL, de Vienne D (1995) Genetic dissection of the relationship between carbon metabolism and early growth in maize, with emphasis on key-enzyme loci. Mol Breed 1:259–272

Cheffings CM, Pantoja O, Ashcroft FM, Smith JAC (1997) Malate transport and vacuolar ion channels in CAM plants. J Exp Bot, Special Issue 48:623–631

Chollet R, Vidal J, O'Leary MH (1996) Phosphoenolpyruvate carboxylase: a ubiquitous, highly regulated enzyme in plants. Annu Rev Plant Physiol Plant Mol Biol 47:273–298

Davies JM (1997) Vacuolar energization: pumps, shunts and stress. J Exp Bot 48:633–641

Dirlewanger E, Pascal T, Zuger C, Kervella J (1996) Analysis of molecular markers associated with powdery mildew resistance genes in peach [*Prunus persica* (L.) Batsch] × *Prunus davidiana* hybrids. Theor Appl Genet 93:909–919

Dirlewanger E, Pronier V, Parvery C, Rothan C, Guy A, Monet R (1998) Genetic linkage map of peach. Theor Appl Genet 97:888–895

Edwards MD, Helentjaris T, Wright S, Stuber CW (1992) Molecular marker-facilitated investigations of quantitative trait loci in maize. Theor Appl Genet 83:765–774

Foolad MR, Arulsekar S, Becerra V, Bliss FA (1995) A genetic map of *Prunus* based on an interspecific cross between peach and almond. Theor Appl Genet 91:262–269

Garvey TC, Hewitt JD (1992) Use of molecular markers to locate quantitative trait loci linked to high soluble-solids content in a hybrid of *Lycopersicon cheesmanii*. J Am Soc Hort Sci 117:497–499

Génard M, Bruchou C (1992) Multivariate analysis of within-tree factors accounting for the variation of peach fruit quality. Sci Hort 52:37–51

Lesley JW (1940) A genetic study of saucer fruit shape and other characters in the peach. Proc Am Soc Hort Sci 37:218–222

Lincoln S, Daly M, Lander E (1992 a) Mapping genes controlling quantitative traits with Mapmaker/QTL 1.1. Whitehead Institute Technical Report, 2ed edn

Lincoln S, Daly M, Lander E (1992 b) Constructing genetic maps with Mapmaker/EXP 3.0. Whitehead Institute Technical Report, 3rd edn

Ma ZQ, Sorrells ME, Tanksley SD (1994). RFLP markers linked to powdery mildew resistance genes *Pm1*, *Pm2*, *Pm3*, and *Pm4* in wheat. Genome 37:871–875

Meredith FI, Robertson JA, Horvat RJ (1989) Changes in physical and chemical parameters associated with quality and postharvest ripening of 'Harvester' peaches. J Agric Food Chem 37:1210–1214

Moing A, Carbonne F, Rashad MH, Gaudillère JP (1992) Carbon fluxes in mature peach leaves. Plant Physiol 100:1878–1884

Moing A, Rothan C, Svanella L, Just D, Diakou P, Rolin D, Gaudillère JP, R Monet (1997) Organic acid metabolism during the fruit development of two peach cultivars. Acta Hort 465:425–432

Monet R (1979) Genetic transmission of the 'non-acid' character. Incidence on selection for quality. In: InRA (ed), Eucarpia Symposium on Tree Fruit Breeding, Angers, pp 273–276

Moriguchi T, Sanada T, Yamaki S (1990) Seasonal fluctuations of some enzymes relating to sucrose and sorbitol metabolism in peach fruit. J Am Soc Hort Sci 115:278–281

Nelson JC (1997) QGENE: software for marker-based genomic analysis and breeding. Mol Breed 3:239–245

Osborn TC, Alexander DC, Fobes JF (1987) Identification of restriction fragment length polymorphisms linked to genes controlling soluble-solids content in tomato fruit. Theor Appl Genet 73:350–356

Pangborn RM (1963) Relative taste intensities of selected sugars and organic acids. J Food Sci 28:726–733

Paran I, Michelmore RW (1993) Development of reliable PCR-based markers linked to downy mildew resistance genes in lettuce. Theor Appl Genet 85:985–993

Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721–726

Plomion C, Liu BH, O'Malley DM (1996) Genetic analysis using trans-dominant linked markers in an F_2 family. Theor Appl Genet 93:1083–1089

Prioul JL, Quarrie S, Causse M, de Vienne D (1997) Dissecting complex physiological functions through the use of molecular quantitative genetics. J Exp Bot 48:1151–1163

Robertson JA, Meredith FI, Russell RB, Scorza R (1989) Physical, chemical and sensory evaluation of high- and low-quality peaches. Acta Hort 254:155–159

Rothan C, Moing A, Just D, Dirlewanger E, Svanella L, Gaudillere JP, Monet R (1997) Isolation and characterization of cDNAs differentially expressed during the early development of peach fruit. Acta Hort 465:99–105

Ruffner HP, Possner D, Brem S, Rast DM (1984) The physiological role of malic enzyme in grape ripening. Planta 160:444–448

Stuber CW, Edwards MD, Wendel JF (1987) Molecular marker-facilitated investigation of quantitative trait loci in maize. II. Factors influencing yield and its component traits. Crop Sci 27:639–648

Tanksley SD, Hewitt J (1988) Use of molecular markers in breeding for soluble-solids content in tomato – a re-examination. Theor Appl Genet 75:811–823

Taureilles-Saurel C, Romieu CG, Robin JP, Flanzy C (1995) Grape (*Vitis vinifera* L.) malate dehydrogenase. II. Characterization of the major mitochondrial and cytosolic isoforms and their role in ripening. Am J Enol Vitic 46:29–36

Tucker GA (1993) Introduction. In: Seymour GB, Taylor JE, Tucker GA (eds) Biochemistry of fruit ripening. Chapman and Hall, London, pp 3–43

Yamaki S, Ishikawa K (1986) Roles of four sorbitol-related enzymes and invertase in the seasonal alteration of sugar metabolism in apple tissue. J Amer Soc Hortic Sci 111:134–137

Yoshida M (1970) Genetical studies on the fruit quality of peach varieties. Bull Hort Res Sta A9 Japon: 1–15