**Analysis of phenotypic variation of sugar profile in different peach
and nectarine [*Prunus persica* (L.) Batsch] breeding progenies**

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Abstract

BACKGROUND: Specific sugar contents are well known for contributing to a range of quality traits of fresh fruits such as flavour, texture and healthy properties. Peaches and nectarines from 205 genotypes coming from 14 different breeding progenies, cultivated under Mediterranean conditions, were evaluated by HPLC for their content of these sugar traits.

RESULTS: A high contribution of cross to the phenotypic variance of all the evaluated fruit quality traits was found. There were significant differences in mean sugar concentrations between peach and nectarine, yellow- and white-fleshed or freestone and clingstone genotypes. Pre-selected genotypes from the original breeding program showed enhanced SSC, total sugar and sucrose contents. Significant effect of year was found for SSC, sucrose and glucose, whereas no effect was found for fructose and sorbitol content. Individual sugar contents correlated significantly with each other and with other fruit quality traits.

CONCLUSION: A significant effect of cross, year and qualitative traits on sugar profile of peaches and nectarines was found. Moreover, the differences showed on sugar traits between the breeding population and the pre-selected genotypes indicated the importance of considering sugar profile on global quality of peaches and nectarines.

Keywords: Brix; fruit breeding; fruit quality; HPLC; sugars

INTRODUCTION

Fruit quality is an abstract concept that varies according to the particular perception of consumers. In recent surveys, inconsistent or poor quality has been mentioned as a major limiting factor influencing consumer choice.¹ Flesh texture and firmness, visual appearance, flavour and aroma are all part of fruit quality as are the levels of sweetness and acidity.² A lack of sugar or sweetness is among the most common consumer complaints in peaches and apricots,³ since composition of sugars ultimately affect fruit quality and flavour.

Recently, peach breeding programmes have stressed the importance of taste in selection of new cultivars.⁴ In our breeding program, we searched for superior peach and nectarine cultivars for the Spanish industry with good adaptation to Mediterranean conditions when grown in the Ebro Valley,⁵ one of the biggest production areas in Europe.⁶ Besides lowering the production costs and improving pest and disease resistance, breeding efforts at this program are directed towards improving both agronomic performance and fruit quality. Soluble sugars are well known for contributing to a range of fruit quality traits such as flavour, texture and healthy properties.² Crisosto and Crisosto⁴ reported that the degree of liking and consumer acceptance were significantly related with SSC, although maximum consumer acceptance was attained at different SSC levels depending on the cultivar. On the other hand, taste is related to water-soluble and non-volatile compounds, while sweetness is mostly attributable to mono- and disaccharides.⁷

The relative content of different sugars present in a given fruit is known as the sugar profile. This term is different to the total sugar content, which is the sum of the most important sugars of a fruit (sucrose, glucose, fructose, and sorbitol). Sucrose is the predominant sugar in the peach fruit.⁸ This disaccharide is important as sweetener,

energy source and antioxidant of fruit flavours.⁹ Other sugars such as glucose, fructose and sorbitol are also present at lower concentrations.¹⁰ Fructose is an important monosaccharide in terms of fruit flavour, since it has a higher level of perceived sweetness than sucrose and glucose.¹¹ Moreover, fructose has been reported to have beneficial effects on gastrointestinal health, since it favors the growth of bifidobacteria and lactobacilli in the gastrointestinal tract.¹² In the field of human nutrition, there is an increasing interest in fruits that are rich in sorbitol, since this sugar alcohol is more beneficial than others with regard to diet control, dental health and gastrointestinal problems.¹³ Sorbitol can be used as a glucose substitute for diabetics and as an alternative natural sweetener instead of sucrose.¹⁴ For these reasons, fruit breeders are also finding specific interest in sorbitol rich fruits.¹³

On the other hand, qualitative pomological traits such as pubescent or glabrous skin (peach or nectarine), round or flat shape, white or yellow flesh and freestone or clingstone, have been studied from the production and marketing point of view. Few investigations have focused on the relationships of these qualitative traits with sugar profile and therefore with fruit taste, and especially in unselected progenies with such variety of fruit types and genetic backgrounds.

This study was undertaken to: (1) evaluate the sugar content and composition of peach and nectarine seedlings and selections from fourteen breeding progenies, (2) study how sugar profile varies with different pomological qualitative traits, such as peach-nectarine, flat-round, flesh colour and/or stone adhesion, (3) determine the year-to-year variations in sugar profile of fruits; and (4) examine relationships among sugar traits and other fruit quality parameters, in order to provide useful information for peach breeding.

80

81 **EXPERIMENTAL**

82 **Plant material**

83 Fourteen controlled biparental crosses between nineteen peach and nectarine
84 cultivars (Table 1) were made during 2000 and 2001. The resulting seedlings were
85 budded on the same rootstock (GF-677) and established (one tree per genotype) in an
86 experimental orchard at the Experimental Station of Aula Dei-CSIC (Northern Spain,
87 Zaragoza) in 2002. Trees were trained to the standard open vase system and planted at a
88 spacing of 4 m x 2.5 m. We minimized environmental sources of variations between
89 genotypes and between fruits within genotype by practicing hand thinning when
90 required. Trees were grown under standard conditions of irrigation, fertilization and pest
91 and disease control. Agronomic and fruit quality traits were evaluated in a total of 205
92 genotypes over three consecutive years (2005-2007). The studied genotypes were
93 selected among the descendants from the 14 crosses for their higher fruit quality or
94 interesting characteristics. All traits were measured or scored for each seedling
95 separately over the 3-year period and means of 3 seasons were calculated. Sugar
96 composition was studied in these 205 genotypes over 2 or 3 years to estimate the
97 seasonal effect on sugar profile. All analyses were carried out on the fruit flesh, since
98 peel is not appreciated by consumers and it is removed prior consumption.

99

100 **Agronomic and fruit quality traits**

101 During the years 2005, 2006 and 2007, agronomic and fruit quality traits were
102 measured individually in each seedling tree. Fruits were considered ripe and hand-
103 picked from the trees when they no longer grew, softened, exhibited yellow or orange

ground colour (which is also representative for each cultivar) and were easily detached. They were harvested by a single person to keep consistency of maturity grade. Depending on genotype, maturity dates ranged from late-May to mid-September. Yield (kg/tree) was determined for each seedling recording also the total number of fruits. From these measurements, the total average fruit weight was calculated. A representative sample of 30 fruits from each plant was randomly selected for the quality evaluations. The agronomic characters segregating as simple characters were recorded, i.e. peach or nectarine, yellow or white flesh, round or flat fruit, aborting or non-aborting fruit, and freestone or clingstone. Some other pomological traits such as skin blush, stone adhesion, endocarp staining and firmness were scored using the rating scales appropriated for each of them. Skin blush was scored as the percentage of skin surface with red color. Endocarp staining (redness around stone) was scored visually on an increasing scale from no color (1) to extremely high redness (10) around the stone. Stone adhesion was scored on an increasing arbitrary scale from totally freestone (1) to strongly clingstone (10). Results for endocarp staining and stone adhesion were expressed as the average value (from 1 to 10) for the 30 evaluated fruits of each genotype. The soluble solids content (SSC) of the juice was measured with a temperature compensated refractometer (model ATC-1, Atago Co., Tokyo, Japan); and data are given as °Brix. The pH and titratable acidity (TA) were measured on the fruit juice. The juice was used crude for pH measurement with a pH electrode, and diluted with de-ionized water for titration to an end pH of 8.1 with 0.1 N NaOH according to the AOAC method.¹⁵ Data are given as g malic acid per 100 g fresh weight (FW), since this is the dominant organic acid in peach.¹⁶ Flesh firmness was determined on opposite sides of the equator of each fruit with a penetrometer fitted with an 8-mm diameter

probe on 5 fruits from each tree. The two readings were averaged per fruit, and data are given in Newtons (N).

Extraction and determination of sugars

Sugar composition was studied in 205 genotypes over 2 or 3 years to estimate the year-to-year variation of sugar profile. Five fruits of each of the 205 seedlings evaluated were peeled with a sharp knife, cut into small pieces, and the flesh was weighted and immediately frozen separately in liquid nitrogen, and stored at -20 °C until analysis. At the moment of analysis, the frozen fruit material (5 g) was homogenized with a Polytron (2 min on ice) with 10 ml of extraction solution, consisting of ethanol/Milli-Q water (80% v/v). The mixture was centrifuged at 20000 x g for 20 min at 4 °C. The supernatant was recovered and assayed by high-performance liquid chromatography (HPLC) as described below.

For sugar analysis, 250 µl of supernatant was incubated at 80 °C for 20 min in 200 µl 80% ethanol, and 5 µg/µl of manitol were added as internal standard. At the end of the incubation, samples were filtered through a Waters C18 cartridge to eliminate any interfering apolar residues. The filters were washed twice with 80% ethanol to elute the retained sugars. Samples were then vacuum concentrated to 500 µl of milliQ water. The obtained solutions were consecutively passed through a 0.45 µm and a 0.22 µm filter to eliminate large particles, prior to analysis on a Ca-column (Aminex HPX-87C 300 mm x 7.8 mm column Bio-Rad) with a refractive-index (RI) detector (Waters 2410). The solvent was vacuum de-gassed deionized water at a flow rate of 0.6 ml min⁻¹ at 85 °C, and 20 µl of the sample were injected into the HPLC. Sugars quantification was performed with the Millenium 3.2 software, Waters (Milford, Mass, USA) using

standards of analytical grade from Panreac Quimica S.A. (Barcelona, Spain). Sugar concentrations were expressed as g per kg of fresh flesh weight (FW).

Statistical analysis

All statistical analyses were performed using SPSS 17.0 for Windows (Chicago, IL). To obtain basic statistics for the entire plant material studied, the number of observed seedlings, maximum and minimum value, mean, mean standard error and standard deviation for each trait were recorded. The significance of cross, year and cross x year interaction effects on sugar contents was tested on the 205 genotypes by analysis of variance. Data for each seedling over the 2 or 3 years of study were averaged, and mean values were used as estimated genotypic values for future analysis. For every quantitative variable, including ordinal scores, the progenies mean were also estimated to find differences between crosses by using Duncan Multiple Range Test ($P \leq 0.05$). When comparing between different fruit types (peach or nectarine, round or flat, yellow or white flesh) the t test ($P \leq 0.05$) was used. The difference on sugar contents between the breeding population and the pre-selected outstanding genotypes was analysed with boxplots drawn. The boxplot can be made to display range, median and distribution density of a variable in a sample size. The median of the data was indicated by the horizontal line in the interior of the box. The height of the box is equal to the interquartile distance, which is the difference between the third quartile of the data and the first quartile. The whiskers extend to a distance (1.5 x inter quartile distance) from the centre. Approximately 99% of the data falls inside the whiskers. The data outside these whiskers are indicated by horizontal lines, and extreme data are indicated by

asterisks. Correlations between traits to reveal possible relationships were calculated from raw data of the 3 years, using the Pearson correlation coefficient at $P \leq 0.05$.

RESULTS AND DISCUSSION

Cross and year effect

The population in this study exhibited considerable phenotypic variation in sugar contents (Table 2). The variation ranges extended between those determined at maturity in *P. persica* by other authors.^{7, 17, 18} In this study, the average content of total sugars (the sum of sucrose, glucose, fructose and sorbitol contents) in the peeled fruit was 72.1 g kg⁻¹ FW. Sucrose, glucose, fructose and sorbitol contents were analyzed separately as they play an important role in peach flavour quality.² Sucrose was the sugar present at the highest concentration in all genotypes evaluated, ranging from 28.2 to 84.4 g kg⁻¹ FW, followed by fructose, glucose and sorbitol. The mean levels of glucose and fructose were quite similar (mean glucose/fructose ratio = 0.8) and about 9 times lower than the mean level of sucrose (mean sucrose/glucose ratio = 9). The range found in sucrose, glucose and fructose among genotypes was 5-fold, while in sorbitol the range was 15-fold. A broad range of SSC (from 7.6 to 17.5 °Brix) was also found among the studied seedlings. On the other hand, a large variation of glucose/fructose ratio (from 0.4 to 2.5) was detected in the studied seedlings. Identifying low glucose/fructose ratio genotypes might be of particular interest, since fructose was rated higher (1.75) than sucrose (1) and glucose (0.75) in terms of sweetness.¹¹ The great genotypic variation in this population suggests that there is a genetic potential to develop peaches and nectarines with improved sugar content. Indeed, 12 of the 26 pre-selected outstanding genotypes showed glucose/fructose ratios lower than 0.7. In agreement, Robertson and

Meredith¹⁹ found that ‘high quality’ peaches contained lower glucose/fructose ratios than ‘low quality’ peaches.

Analysis of variance on the 205 genotypes over 3 years of study (Table 3) showed that cross and year significantly affected all evaluated traits, except for fructose and sorbitol content, which were not significantly affected by year. These results suggest that fructose and sorbitol contents appear to be less influenced by the prevailing environmental conditions over the growing season than the other fruit quality traits evaluated. Anyway, contribution of year to the phenotypic variance of sucrose and glucose contents was low (2.2% and 1.7%, respectively), whereas the phenotypic variance of SSC explained by year was higher (17.4%). In peach, a year effect has been reported for SSC, sucrose, glucose and sorbitol contents.^{18, 20} The year-to-year variation in sugar profile may be explained by the differences in climate and crop load over the 3 years of study.²⁰ Several studies have previously characterized *Prunus* populations for patterns of variation in sugar contents.^{18, 21} These studies agree that environment influences the level of individual sugars (sucrose, glucose, fructose, and sorbitol) although sugar profile seems to be relatively constant across environments. Statistically significant cross x year interactions were only observed for fruit weight and pH. Due to the not significant cross x year interactions on the SSC, TA and individual sugar contents, the data from different years were analysed together.

The significant effect of cross found for all the evaluated traits and its high contribution to their phenotypic variance (Table 3), agree with previous works where cross effect on peach quality have been reported.²⁰ The highest SSC was shown by the O’Henry x VAC-9515 progeny (Table 4), without being statistically different from the other two progenies descendant from O’Henry, Andross x Calante, Andross x VAC-9511, Rich Lady x VAC-9511 and VAC-9520 x VAC-9517 progenies. On the contrary,

223 Babygold-9 x Crown Princess showed the lowest SSC, without showing significant
224 differences with Andross x Crown Princess, Andross x Rich Lady, Babygold-9 x VAC-
225 9510 and Redtop x VAC-9513 progenies. SSC is an important quality trait in peaches
226 and nectarines since it has been related with the degree of liking and consumer
227 acceptance.⁴ Consumer acceptance of high acid cultivars have been reported to increase
228 as SSC increases, until reaching a plateau (at 11-12 °Brix) above which it becomes
229 insensitive to any additional increase in SSC.⁴ However, this plateau has not been found
230 for the low acid cultivars. On the other hand, the relationship between sugar
231 composition and consumer acceptance is cultivar specific, and there is not a single
232 reliable SSC or sugar content value which assures consumer satisfaction across all
233 cultivars and consumer preferences.²² Average total sugar content in the Andross x
234 Calante progeny was greater than in other progenies in the observed period. However,
235 no significant differences were found with other progenies such as Andross x Rich
236 Lady, the three progenies descendant from O'Henry cultivar, VAC-9512 x VAC-9511
237 and VAC-9520 x VAC-9517. In contrast, the Redtop x VAC-9513 progeny showed the
238 lowest mean of total sugars content, being significant different from Andross x Calante,
239 O'Henry x VAC-9514, O'Henry x VAC-9515 and VAC-9512 x VAC-9511 progenies.
240 Total sugars content is an important quality trait in the fruit breeding programs, since it
241 has been reported to be highly related to aroma and taste of peaches and nectarines.⁷ Big
242 differences were also found among progenies in the sorbitol content, ranging from 1.4 g
243 kg⁻¹ FW in Andross x Crown Princess to 5.3 g kg⁻¹ FW in O'Henry x VAC-9514.
244 Consequently, the percentage of sorbitol in the sugar composition was significantly
245 different among progenies, ranging from 2.1% to 7.1%. However, the mean sorbitol
246 content remained lower than 10 g kg⁻¹ FW for all the progenies in agreement with the
247 sorbitol values found in peaches and nectarines.²³ Due to the important role of sorbitol

in the texture and flavour of peach and nectarine fruits, this interesting trait was valued, among others, in the selection of two genotypes from the O’Henry x VAC-9514 progeny. Colaric et al.⁷ reported that sorbitol was the attribute most related to peach aroma and taste among carbohydrates and organic acids. Moreover, it is an interesting polyalcohol in terms of nutrition for special dietary purposes, such as diet control or dental health.¹⁴ Therefore, genotypes with high sorbitol content are nowadays interesting for fruit breeders.¹³ Glucose/fructose ratios were near one for most progenies, since seasonal changes in glucose and fructose contents have the same pattern and they are usually similar in amount in peach and nectarine fruits.²⁴ However, significant differences among crosses were found for this ratio, obtaining values from 0.65 in Andross x Calante and Andross x Rich Lady progenies, to 1.05 in O’Henry x VAC-9516 progeny.

As a result of the evaluations carried out on the ongoing breeding program, 26 superior genotypes were pre-selected from the whole breeding population. The selection was performed by independent culling of the most important agronomic (harvest date and yield) and fruit quality traits (fruit weight, fruit shape, soluble solids content, acidity, skin blush, endocarp staining, firmness, flavor, texture, and chilling injury susceptibility). A graphical representation showing the median and spread of the distribution of sugar contents of the 205 seedlings of the breeding population (set I) and the 26 pre-selected outstanding genotypes (set II) is given in Figure 1. Compared with set I, genotypes in set II showed lower variations due to the selection process. Mean sucrose content was significantly higher ($P \leq 0.01$) in set II than in set I. Although not significant differences were found between both sets for the mean contents of glucose, fructose and sorbitol, 12 and 8 outstanding pre-selected genotypes (data not shown) had fructose and sorbitol values respectively, over the evaluated population (8.6 g kg^{-1} and

3.0 g kg⁻¹, respectively). Significant higher SSC ($P \leq 0.05$) and total sugar content ($P \leq 0.01$) was also found in set II when comparing with set I, indicating that progress has been made in our breeding program toward selection of higher sugar content fruits. The significant differences on several sugar traits observed between the pre-selected genotypes and the breeding population confirm the effect of sugar composition on the sensorial quality of the peach fruit,^{4, 7} since selection of outstanding seedlings was based on various fruit quality traits which may be influenced by, but are not only restricted to the sugar profile. The results show the indirect contribution of sugar profile as a trait in the selection of the best genotypes. Harker *et al.*²⁵ compared instrumental and sensory measurements of apple taste, and reported that SSC was the best predictor of sweet taste. Karakurt *et al.*²⁶ related the lack of flavour of melting peaches with reduced SSC and total sugars. However, the relationship between SSC and consumer acceptance is cultivar specific, and there is not a single reliable SSC that assures consumer satisfaction.⁴ The difference in sucrose content between sets I and II, corroborates the importance of sucrose on the sensorial peach and nectarine quality. Colaric *et al.*⁷ reported a high contribution of sucrose to aroma and taste of peach and nectarine fruits, indicating that peach fruits with better aroma ratings had also higher sucrose contents. Moreover, sucrose is important as energy source and as a preservative of fruit flavours.⁹

Qualitative traits effect

Different qualitative pomological traits were studied to reveal their possible relationships with the sugar profile of peaches and nectarines (Table 5). In the case of pubescent *vs.* glabrous skin, nectarine fruits showed significantly higher SSC, glucose, total sugars and glucose/fructose ratio than peach fruit, in agreement with other

authors.²³ Due to their higher glucose content, significant lower sucrose/glucose ratio was found in nectarines than in peaches. Nevertheless, no significant differences between peach and nectarine fruits were observed for sucrose, fructose and sorbitol contents. Similarly to our results, Day et al.²⁷ found that 15 peach cultivars averaged approximately 11 °Brix SSC, whereas 11 nectarine cultivars averaged approximately 14 °Brix SSC. Moreover, a trained taste panel found that nectarine cultivars were sweeter than peach cultivars. All these results show the advantages of nectarines over peaches in relation to sugar concentrations, although cultivar variations should be also taken into account. The co-localization of major QTLs controlling SSC with the morphological marker for peach vs. nectarine fruit on linkage group 5 (LG5)^{28, 29} may partly explain the observed differences.

Significant differences in sugar contents were also found when comparing yellow and white flesh colour fruits. White flesh fruits showed significantly higher SSC, individual and total sugar contents (Table 5) than yellow flesh fruits, in agreement with Robertson *et al.*⁸ who reported higher sucrose, glucose, fructose and SSC in white-fleshed than in yellow-fleshed peaches. A similar tendency was also found by Wu *et al.*³⁰ who reported that mean sucrose concentrations in white-fleshed genotypes were about 10% higher than those in yellow-fleshed genotypes. The identification of QTLs controlling fructose content and sweetness²⁹ co-localizing with the morphological marker for yellow/white flesh³¹ on LG1 might explain the linked segregation of both traits. However, to our knowledge, few studies have focused on the relationship between fruit flesh colour and sugar concentrations. It is assumed that white- and yellow-fleshed fruit differ in acidity and sugar composition and this may contribute to the different preferences shown by groups of consumers. In general, Asian consumers prefer white-fleshed cultivars that are considered to have lower acidity and higher

sweetness, while yellow-fleshed peaches are often favoured in Europe and America.²⁷ However, nowadays and due to the increasing gene exchange between different cultivars occurred on the peach breeding programs, it is also possible to find white-fleshed peaches with lower sweetness and higher acid levels.

In our program, there is only one progeny (VAC-9520 x VAC-9517) segregating for the fruit shape trait (flat vs. round). In this population, flat fruit genotypes showed significant higher SSC (13.7 °Brix) than round ones (11.3 °Brix) (Table 5), even when compared to the round fruit within the same progeny (11.5 °Brix). Higher individual and total sugar contents were also found in flat fruits although differences were not significant. This result agrees with previous works, where flat peach varieties have been reported to have excellent flavour with a sweet taste, low titratable acidity and high sugar content.³² This could be explained by the localization of QTLs for SSC¹⁸ and total sugars²⁸ on LG6, near the dominant gene (S, for ‘saucer-shaped’) controlling the flat fruit character³³.

In the case of the freestone-clingstone trait, significantly higher SSC, total sugar and individual sugar contents were found in freestone fruits (Table 5). These differences may be explained by the identification on LG4 of QTLs involved in SSC, glucose and sucrose contents,²⁹ near the physical trait controlling flesh adhesion to the stone (F/f). Also the selection pressure for higher sugar contents on breeding programs for peach freestone cultivars for fresh market may contribute to these results. No differences between both types of fruits were reported in a previous work with a *P. persica* x *P. davidiana* breeding progeny.²³ Flesh adhesion to the stone in peach and nectarine is an important quality trait which determines fruit usage (canning, drying or table fresh fruits). Therefore, relationships between this trait and sugar concentrations may be useful in breeding strategies. However, until now, studies on the relationship between

flesh adhesion and fruit flavour have been scarce. The present study shows a possible functional link between flesh adhesion and sugar profile of peaches and nectarines. Further studies on this aspect would be of interest for peach breeding.

Correlations between sugar contents and other fruit quality traits

In order to find markers for breeding purposes, we calculate the correlation coefficients between sugar and other evaluated fruit quality traits (Table 6). All sugar contents studied were positively correlated between each other and with other fruit composition traits, which could be partly explained by the location of QTLs for nearly all the chemical compounds (sucrose, fructose, sorbitol, malic and citric acid) in linkage groups 5 and 6.¹⁸ Among individual sugars, the highest correlation was found between glucose and fructose ($r = 0.50^{**}$), as reported by other authors.^{18, 24} Several authors have shown that seasonal changes in glucose and fructose contents had the same pattern and they had approximately equal amounts during fruit development.³⁴ The correlations found in our study were lower than those reported by Esti et al.² and Dirlewanger et al.¹⁸ because, although most genotypes had higher fructose content than glucose content, some of them were characterized by a higher content of glucose as shown by Wu et al.²⁴ and Moriguchi et al.¹⁰ This indicates that independent genetic control of both sugar contents may exist. Sorbitol correlated significantly with the rest of individual sugar contents as previously reported,²⁴ since even though the absolute sugar contents vary, sugar profile remains generally stable among genotypes,¹³ and therefore, higher total sugar content fruits will also have higher glucose, fructose and sorbitol contents.

Total sugars had a highly significant correlation with sucrose ($r = 0.94^{**}$), as this is the predominant soluble sugar at maturity (20-90 g kg⁻¹ FW) in *P. persica* fruit.¹⁸ SSC was also positively correlated with sucrose, glucose, fructose and sorbitol as

observed in other peach and nectarine cultivars.²⁴ Correlation between SSC and total sugars was not very high ($r = 0.33^{**}$), as reported for citrus³⁵ and other peach cultivars,³⁶ probably due to the contribution of other soluble optically active compounds different from sugars such as pectins, salts and organic acids to SSC value. Indeed, high correlations have been found between SSC and organic acids.²⁴ However, correlation coefficients varied depending on the progeny, being higher in progenies such as VAC-9512 x VAC-9511 ($r = 0.51^{**}$) and Babygold-9 x Crown Princess ($r = 0.52^{**}$), indicating a higher contribution of sugars to the SSC of their fruit.

Yield showed a negative significant correlation with SSC, obtaining higher coefficients in progenies such as Rich Lady x VAC-9511 ($r = -0.50^{**}$), Andross x Crown Princess ($r = -0.39^{**}$) and VAC-9520 x VAC-9517 ($r = -0.53^{**}$). Similar results were found when the whole breeding population (1111 genotypes) was analyzed³⁷. This relationship could be explained by the negative effect of high crop loads on the total sugar content of fruits, as shown by Morandi et al.³⁸ These authors demonstrated that high crop loads induced lower fruit total sugar content due to sink competition among fruits. On the other hand, fruit weight showed, in general, positive correlations with sugar levels. Slight significant correlation was found between fruit weight and SSC when all the seedlings were evaluated, and higher coefficients were found for certain progenies such as Andross x Rich Lady ($r = 0.58^{**}$), Andross x Crown Princess ($r = 0.47^{**}$) and O'Henry x VAC-9516 ($r = 0.46^{**}$). Similarly, a significant loose correlation was found between fruit weight and total sugar content, with higher coefficients for some progenies such as Babygold-9 x Crown Princess ($r = 0.49^{**}$) and Red Top x VAC-9513 ($r = 0.36^{**}$). These results are expectable since amount of translocated carbohydrates determines fruit growth rate as demonstrated by Morandi et al.³⁸ Thus, although the fruit growth rate is not only determined by the

availability of assimilates, a high carbon supply to the fruit as a sink organ will result into higher growth rates. At the same time, fruit sink size, together with sink activity, determines sink strength to attract sucrose and sorbitol from the leaves.³⁸

Other positive significant correlations were found between sugar components and other quality traits such as skin blush, endocarp staining, TA, RI and/or firmness. The positive significant correlation found between some sugar traits with skin blush and endocarp staining, indicates that besides the positive effect of blush and endocarp staining on attractiveness and healthy promoting properties of fruits,³⁹ these traits could be related to higher SSC and total sugars content, and therefore to better organoleptic quality. This relationship is reasonable since a sufficient accumulation of assimilates, contributing to the SSC, in or near the fruit is essential for phenolic compounds synthesis, responsible of the blush and endocarp staining of fruits.⁴⁰ Titratable acidity showed a significant positive correlation with sucrose, glucose, fructose, sorbitol, total sugars and SSC, in agreement with previous works.²⁴ This result could be due to the co-localization of QTLs involved in fruit weight, SSC, sugars and acid contents in peach.¹⁸ An expectable high correlation was found between RI and SSC, since RI is the ratio between SSC and TA. This sugar-acid ratio (RI) is commonly used as a quality index, and higher ratios are usually indicative of higher and more acceptable fruit quality⁴ since it has been reported that RI is better correlated with perceived sweetness than individual sugars.⁷ On the other hand, firmness show a significant loose correlation ($r = 0.27$) with SSC, and other sugar traits. This means that, for the same state of ripening, firmer fruits could have higher SSC and total sugar content, in agreement with what has been reported for sweet cherry.⁴¹

CONCLUSIONS

On the basis of this study, the substantial variation among the breeding genotypes suggest that high quality peach and nectarine genotypes based on sugar contents can be developed in the future. The results showed the significant influence of cross, year, and different qualitative pomological traits on sugar profile of peaches and nectarines. Due to the high total sugar content, the low glucose/fructose ratio and the high percentage of sorbitol found in its progeny, O'Henry turned out to be an interesting cultivar to be used as a parent on breeding programs searching for high quality peaches and nectarines. Nectarine and flat fruits showed a tendency of having higher SSC and total sugars content than peaches and round fruits, respectively. Also, white flesh fruits had in general, higher sugar values than yellow flesh fruits. A slight tendency was also observed for free-stone fruit type to have higher SSC, total sugars and individual sugar contents than cling-stone fruit type. On the other hand, a year effect was found for fruit weight, SSC, TA, sucrose and glucose contents, whereas fructose and sorbitol appear to be less variable across environments. Valuable correlations among agronomic and fruit quality parameters and sugar traits were found, although coefficients variation depending on the progeny should be considered. The results of this work show the importance of the sugar profile as a trait to be considered in a breeding program searching for high quality peaches and nectarines. Further, our results show the extent of sugar profile modification feasible in the peach and nectarine germplasm adapted to the Mediterranean area.

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TABLES

Table 1. Peach and nectarine commercial and experimental (VAC-) cultivars used as progenitors in the 14 controlled crosses. Fruit type (round or flat, peach or nectarine), flesh colour (yellow or white), and stone adhesion (free or cling) for each progenitor is shown.

Cultivar	Fruit type		Flesh colour	Stone
Andross	round	peach	yellow	cling
Babygold-9	round	peach	yellow	cling
Calante	round	peach	yellow	cling
Crown Princess	round	peach	yellow	cling
O'Henry	round	peach	yellow	free
Orion	round	peach	yellow	free
Red Top	round	peach	yellow	free
Rich Lady	round	peach	white	free
VAC-9510	round	peach	yellow	cling
VAC-9511	round	peach	yellow	free
VAC-9512	round	peach	yellow	free
VAC-9513	round	nectarine	yellow	free
VAC-9514	round	nectarine	white	free
VAC-9515	round	nectarine	yellow	free
VAC-9516	round	peach	white	free
VAC-9517	flat	peach	white	free
VAC-9520	round	peach	yellow	free

Table 2. Soluble solids content (SSC), individual sugars, total sugar contents and specific sugar ratios rates for the seedlings from 14 peach and nectarine breeding progenies studied over 3 years. For each trait, number of observed seedlings (n), minimum, maximum, mean value, mean standard error (MSE), and standard deviation (SD) are presented.

Sugar trait	n	Minimum	Maximum	Mean	MSE	SD
SSC (°Brix)	205	7.6	17.5	11.5	0.12	1.7
Sucrose (g kg ⁻¹ FW)	205	28.2	84.4	54.3	0.79	11.3
Glucose (g kg ⁻¹ FW)	205	2.3	14.6	6.5	0.13	1.9
Fructose (g kg ⁻¹ FW)	205	3.8	16.1	8.6	0.15	2.2
Sorbitol (g kg ⁻¹ FW)	205	0.9	10.6	3.0	0.14	2.0
Total sugars ^a (g kg ⁻¹ FW)	205	36.0	109.4	72.1	0.99	14.2
Sucrose/Glucose	205	2.7	18.9	9.0	0.19	2.7
Glucose/Fructose	205	0.4	2.5	0.8	0.02	0.3
% Sorbitol	205	1.2	14.3	4.1	0.17	2.4

^a Total sugars: the sum of sucrose, glucose, fructose, and sorbitol for each genotype, analyzed by HPLC

Table 3. F values and proportion (%) of phenotypic variance obtained in the ANOVA for the studied factors in the seedlings from 14 F1 peach progenies.

Variable	DF	MS	F-value	P	phenotypic variance (%)
Fruit weight					
Cross	13	46769.12	30.85	0.000	52.2
Year	2	23496.62	15.50	0.000	7.8
Cross x Year	22	3003.47	1.98	0.006	10.6
Error	368	1515.94			
TA					
Cross	13	0.44	17.26	0.000	37.9
Year	2	0.13	5.11	0.007	2.7
Cross x Year	22	0.02	0.84	0.673	4.8
Error	368	0.03			
pH					
Cross	13	0.46	12.01	0.000	29.8
Year	2	5.89	153.78	0.000	45.5
Cross x Year	22	0.07	1.92	0.008	10.3
Error	368	0.04			
SSC					
Cross	13	32.22	14.17	0.000	33.4
Year	2	88.08	38.74	0.000	17.4
Cross x Year	22	1.72	0.75	0.781	4.3
Error	368	2.27			
Sucrose					
Cross	13	625.19	4.95	0.000	14.9
Year	2	514.76	4.08	0.018	2.2
Cross x Year	22	90.93	0.72	0.819	4.1
Error	368	126.22			
Glucose					
Cross	13	13.67	3.97	0.000	12.3
Year	2	11.00	3.19	0.042	1.7
Cross x Year	22	1.65	0.48	0.980	2.8
Error	368	3.45			
Fructose					
Cross	13	24.05	5.62	0.000	16.6
Year	2	1.66	0.39	0.679	0.2
Cross x Year	22	2.73	0.64	0.897	3.7
Error	368	4.28			
Sorbitol					
Cross	13	35.10	10.91	0.000	27.8
Year	2	2.04	0.63	0.531	0.3
Cross x Year	22	1.73	0.54	0.958	3.1
Error	368	3.22			

Table 4. Soluble solids content (SSC, °Brix), individual sugars, total sugars contents (g kg⁻¹ FW), and specific sugar ratios of fruits of 14 breeding progenies averaged for each studied progeny. The number of observed seedlings (n) for each progeny is presented. Values are means of 2 or 3 years of study.

Progeny	n	SSC	Sucrose	Glucose	Fructose	Sorbitol	Total sugars*	Sucrose/ Glucose	Glucose/ Fructose	% Sorbitol
Andross x Calante	19	12.2 abc	64.0 a	6.6 ab	10.3 a	5.1 a	85.9 a	10.0 a	0.65 b	5.9 ab
Andross x Crown Princess	9	11.0 cde	51.6 bc	6.4 ab	7.6 ab	1.4 g	67.0 cd	8.5 ab	0.86 ab	2.1 e
Andross x Rich Lady	9	11.1 cde	54.9 abc	5.8 b	9.0 ab	3.6 abcde	73.3 abcd	9.7 ab	0.65 b	4.8 bcd
Andross x VAC-9511	6	11.9 abc	49.6 c	6.7 ab	9.1 ab	1.6 fg	67.0 cd	8.1 ab	0.73 b	2.5 e
Babygold-9 x Crown Princess	19	9.7 e	53.5 abc	5.7 b	7.9 ab	2.4 cdefg	69.4 bcd	9.8 a	0.73 b	3.4 cde
Babygold-9 x VAC-9510	15	11.0 cde	52.5 bc	5.7 b	7.4 ab	2.2 defg	67.7 bcd	9.7 ab	0.79 ab	3.2 de
O'Henry x VAC-9514	14	13.2 ab	54.3 abc	8.0 a	10.1 a	5.3 a	77.7 abc	7.0 b	0.79 ab	7.1 a
O'Henry x VAC-9515	8	13.5 a	60.9 ab	6.8 ab	9.3 ab	3.2 bcdef	80.3 ab	9.3 ab	0.85 ab	4.0 cde
O'Henry x VAC-9516	11	12.5 abc	58.2 abc	6.5 ab	6.9 c	3.9 abc	75.5 abcd	9.8 a	1.05 a	5.1 abcd
Orion x VAC-9510	3	11.6 bcd	47.1 c	7.3 ab	8.9 abc	3.9 abcd	67.2 bcd	7.4 ab	0.82 ab	5.4 abc
Red Top x VAC-9513	37	9.9 de	48.4 c	5.6 b	7.8 ab	2.1 efg	64.0 d	9.6 ab	0.75 b	3.4 cde
Rich Lady x VAC-9511	8	12.3 abc	50.0 bc	6.7 ab	8.4 abc	2.5 bcdefg	67.6 bcd	7.6 ab	0.81 ab	3.6 cde
VAC-9512 x VAC-9511	10	11.6 bcd	57.1 abc	7.0 ab	9.0 bc	4.2 abcd	77.3 abc	8.6 ab	0.79 ab	5.3 abcd
VAC-9520 x VAC-9517	37	12.2 abc	56.5 abc	7.3 ab	8.9 abc	2.8 bcdefg	75.6 abcd	8.5 ab	0.84 ab	3.7 cde

Mean separation in columns by Duncan's test ($P \leq 0.05$). In each column, values with the same letter are not significantly different.

*Total sugars: the sum of sucrose, glucose, fructose, and sorbitol for each genotype, analyzed by HPLC

Table 5. Soluble solids content (SSC, °Brix), individual sugars, total sugars contents (g kg⁻¹ FW), and specific sugar ratios associated with qualitative traits in peach and nectarine genotypes from 14 breeding progenies. The number of observed seedlings (n) for each fruit type is presented. Values are means of 2 or 3 years of study.

Traits	n	SSC	Sucrose	Glucose	Fructose	Sorbitol	Total sugars*	Sucrose/ Glucose	Glucose/ Fructose	% Sorbitol
Peach	191	11.3 b	54.8 a	6.4 b	8.6 a	3.1 a	72.6 b	9.1 a	0.78 b	4.2 a
Nectarine	14	14.1 a	57.6 a	7.6 a	8.9 a	3.0 a	77.1 a	7.8 b	0.88 a	3.8 a
Yellow-fleshed	163	11.2 b	53.7 b	6.3 b	8.4 b	2.9 b	71.3 b	9.1 a	0.77 b	4.0 b
White-fleshed	42	12.3 a	56.9 a	7.4 a	9.1 a	3.8 a	77.2 a	8.6 a	0.86 a	4.8 a
Round	190	11.3 b	54.7 a	6.5 a	8.6 a	3.1 a	73.0 a	9.0 a	0.79 a	4.2 a
Flat	15	13.7 a	58.7 a	6.8 a	9.1 a	3.1 a	77.7 a	9.5 a	0.76 a	3.9 a
Freestone	28	12.9 a	59.3 a	7.1 a	9.3 a	4.5 a	80.2 a	8.9 a	0.80 a	5.5 a
Clingstone	177	11.3 b	54.3 b	6.4 b	8.5 b	2.9 b	71.8 b	9.1 a	0.78 a	4.0 b

Mean separation in columns by *t*-test ($P \leq 0.05$). For each trait, in the same column, values with the same letter are not significantly different.

*Total sugars: the sum of sucrose, glucose, fructose, and sorbitol for each genotype, analyzed by HPLC

Table 6. Correlation coefficients between traits in the 205 peach and nectarine genotypes of the 14 studied populations over 3 years. Correlation coefficients were calculated with one mean value per genotype.

Trait	SSC	Sucrose	Glucose	Fructose	Sorbitol	Total sugars ^a
Sucrose	0.26 **					
Glucose	0.25 **	0.21 **				
Fructose	0.22 **	0.24 **	0.50 **			
Sorbitol	0.33 **	0.27 **	0.31 **	0.46 **		
Total sugars	0.33 **	0.94 **	0.43 **	0.49 **	0.49 **	
Yield	-0.21 **	NS	NS	NS	-0.16 **	NS
Fruit weight	0.12 **	NS	NS	0.12 *	0.19 **	0.13 **
Blush %	0.14 **	NS	0.13 **	NS	NS	NS
Endocarp staining ^b	0.21 **	NS	NS	0.12 *	0.18 **	0.13 **
pH	NS	-0.11 *	-0.11 *	NS	0.10 *	NS
TA	0.37 **	0.10 *	0.21 **	0.11 *	NS	0.14 **
RI	0.53 **	0.13 **	NS	0.12 *	0.14 **	0.16 **
Firmness	0.27 **	NS	NS	0.13 *	0.17 **	0.12 *

* and ** represent statistical significance at $P \leq 0.05$ and $P \leq 0.01$ respectively. NS, not significant.

Abbreviations: SSC, soluble solids content; TA, titratable acidity; RI, ripening index (SSC/TA)

^a Total sugars: the sum of sucrose, glucose, fructose, and sorbitol for each genotype, analyzed by HPLC

^b Ten-step scale from no endocarp staining (1) to strongly red staining (10)

Figure 1. Range and distribution of sugars in the 205 seedlings of the breeding population (set I) and in the 26 pre-selected outstanding seedlings (set II). The horizontal lines in the interior of the box are the median values. The height of the box is equal to the interquartile distance, indicating the distribution for 50% of the data. Approximately 99% of the data falls inside the whiskers (the lines extending from the top and bottom of the box). The data outside these whiskers are indicated by horizontal lines. * and ** represent significant differences for each trait between set I and II at $P \leq 0.05$ and $P \leq 0.01$ respectively. NS, not significant differences.

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