Fructose Content and the Activity of Fructose-related Enzymes in the Fruit of Eating-quality Peach Cultivars and Native-type Peach Cultivars

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Summary

Significant differences in fructose content were detected among different cultivars of the peach (*Prunus persica* (L.) Batsch). To investigate the factors that regulate fructose concentrations in peach fruit, we measured the activities of fructose-related enzymes in two eating-quality peaches, 'Akatsuki' and 'Kawanakajima hakuto', and two native-type peaches, 'Nagano yaseito Early' and 'Noto zairaito No. 2'. Fructose contents in the fruit of the eating-quality peach cultivars, measured from 3 months after flowering to the ripe stage, ranged from 7 to 12 mg·g⁻¹ FW, whereas those of the native-type peach cultivars were less than 1 mg·g⁻¹ FW. There were no clear differences between the two groups with respect to fructokinase, fructose-6-phosphatase, and phosphoglucose isomerase (PGI) enzyme activities although they were low in 'Noto zairaito No. 2'. In all cultivars, the activity of PGI was much higher than that of the other enzymes. This finding suggests that isomerization by PGI is not the rate-limiting step in the synthesis of fructose. The concentration of fructose-6-phosphate (Fru6P) in the fruit did not differ between the two groups. These results suggest that the differences in fructose content in different peach cultivars are related to different capacities for fructose production rather than to differences in the ability to convert fructose to Fru6P and then to glucose-6-phosphate. NAD-dependent sorbitol dehydrogenase (SDH) activity was found to be higher in the eating-quality peach cultivars than in the native-type peach cultivars during all fruit development stages tested in this study. It is therefore likely that SDH, which contributes to the production of fructose from sorbitol, is responsible for the regulation of fructose concentrations in peach fruit.

Key Words: fructose, fruit, peach, sorbitol dehydrogenase, sugar.

Introduction

Glucose, fructose, and sucrose are the major sugars found in common fruits. Fructose is the sweetest of the major sugars; therefore, its concentration is the most likely factor to affect the taste of the fruit (Schaffer et al., 1999). Levin et al. (2000) described an *Fgr* locus that modulates the ratio of fructose to glucose in mature tomato (*Lycopersicon esculentum* Mill.) fruits. However, the biochemical mechanism, responsible for the modulation of fructose concentration by *Fgr*, remains unclear. For other fruits, very little is known regarding the factors that regulate fructose concentration.

Moriguchi et al. (1990a), who reported significant differences in the sugar composition of different peach (*Prunus persica* (L.) Batsch) fruit cultivars, found that, in 34 eating-quality cultivars and 20 native-type cultivars, fructose was present in comparatively low concentrations in native-type peach cultivars as compared with eating-quality cultivars. In this study, we analyzed two

cultivars each from the eating-quality and native-type peaches for several physiological characteristics in an attempt to identify the factors that affect fructose concentrations in peach fruit.

The concentration of sorbitol in peach phloem sap (560 mM) is approximately four times the sucrose concentration (Moing et al., 1997). Fructose is synthesized from sorbitol by an NAD-dependent sorbitol dehydrogenase (SDH) in peach fruit (Yamada et al., 2001) (Fig. 1). SDH is known to play an important role in sink tissues such as fruit (Lo Bianco and Rieger, 2002). Fructose is synthesized by SDH and is phosphorylated by an enzyme, fructokinase (FRK) (Fig. 1). In this study we investigated the relation between fructose content and the activities of fructose-related enzymes, such as SDH and FRK, for a range of peach cultivars.

Materials and Methods

Plant materials

In this study, fruits of eating-quality peaches 'Akatsuki' and 'Kawanakajima hakuto' and fruits of native-type peaches 'Nagano yaseito Early' and 'Noto

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Fig. 1. Proposed pathway of sorbitol metabolism and sucrose synthesis in peach fruit. Enzymes referred in the discussion are shown. The arrows indicate the main direction of each reaction in the pathway. SDH, sorbitol dehydrogenase; FRK, fructokinase; Fru6Pase, fructose-6-phosphatase; PGI, phosphoglucose isomerase; SuSy, sucrose synthase.

zairaito No. 2' were harvested periodically 3 months after flowering to harvest at the ripe stage. Harvested fruit flesh was stored at -80°C before analysis.

Determination of soluble-carbohydrate and hexose phosphate contents

Soluble carbohydrates were extracted and analyzed as described by Odanaka et al. (2002), while glucose-6-phosphate (Glc6P) and fructose-6-phosphate (Fru6P) were extracted from frozen tissues and analyzed according to Tobias et al. (1992). Pigments were removed with Sep-Pak C_{18} Cartridges (Waters, Milford, MA) or activated carbon.

Enzyme activity analyses

SDH was extracted from the tissues and assayed according to protocols described by Lo Bianco and Rieger (2002). For the measurement of SDH, 250 mM sorbitol served as the substrate.

FRK, fructose-6-phosphatase (Fru6Pase), and phosphoglucose isomerase (PGI) were extracted at 4°C according to Schaffer and Petreikov (1997). Fruit flesh was ground to a powder in the presence of liquid nitrogen. The powder was then extracted with 50 mM Hepes-NaOH (pH 7.5), containing 1 mM MgCl_2 , 1 mM EDTA, 10 mM KCl, 2.5 mM dithiothreitol, 3 mM sodium *N,N*-diethyldithiocarbamate trihydrate, 0.5% (w/v) polyvinylpolypyrrolidone, and 1% (w/v) bovine serum albumin. The homogenate was centrifuged for 15 min at $10000 \times g$, and the supernatant fraction was filtered. The filtrate was precipitated with the addition of 80% ammonium sulfate and the mixture centrifuged for 15 min at $10000 \times g$. The precipitate was resuspended in the extraction buffer, which did not contain polyvinylpolypyrrolidone or bovine serum albumin, and was then desalted on an NAP 10 column (Amersham Biosciences, USA).

FRK activity was assayed according to the method of Martinez-Barajas and Randall (1996). The fructose concentration in the reaction mixture was either 50 or 0.5 mM. Fru6Pase activity was analyzed according to Morton et al. (1985). Either 60 mM Hepes-NaOH (pH 7.2) or 60 mM acetate-NaOH (pH 5.0) was used as the reaction buffer in this assay. PGI activity was measured by the method of Schaffer and Petreikov (1997).

Fig. 2. Changes in the soluble-carbohydrate content of different peach cultivars. Fructose, glucose, sorbitol, and sucrose concentrations were measured in the fruit of eating-quality peaches 'Akatsuki' and 'Kawanakajima hakuto' and of native-type peaches 'Nagano yaseito Early' and 'Noto zairaito No. 2'. Each value represents the mean of triplicate measurements and the associated SE.

Results

Soluble-carbohydrate composition

The fructose content of the eating-quality peaches 'Akatsuki' and 'Kawanakajima hakuto' was approximately $10 \text{ mg} \cdot \text{g}^{-1} \text{FW}$ 3 months after flowering and remained constant until harvest (Fig. 2). The fructose content of the native-type peaches 'Nagano yaseito Early' and 'Noto zairaito No. 2' remained at $0\text{--}1 \text{ mg} \cdot \text{g}^{-1} \text{FW}$ 3 months after anthesis to harvest.

The glucose and sorbitol contents of 'Akatsuki', 'Kawanakajima hakuto', and 'Noto zairaito No. 2' were similar at all stages of fruit development tested in this study, whereas sucrose was the most abundant soluble carbohydrates in the fruit tissues (Fig. 2). The sucrose content was significantly higher in the eating-quality peach cultivars than in the native-type ones.

Enzyme activity

Kanayama et al. (1998) identified two FRK genes (*Frk1* and *Frk2*) in tomato plants. The product of *Frk1* has a high K_m value (1.3 mM) and does not show substrate inhibition. Fifty mM fructose was therefore added to the reaction mixture before the measurement of maximum activity of *Frk1*-type FRK. In contrast, the product of *Frk2* has a low K_m value (0.054 mM) and

causes substrate inhibition. The activity of *Frk2* is significantly inhibited by the addition of 50 mM fructose. Therefore, comparatively low concentrations of fructose are required for measuring the maximum activity of *Frk2*-type FRK. In this study, FRK activity was assayed in a reaction mixture that contained fructose

Fig. 3. Changes in the fructokinase (FRK) activity of eating-quality peaches 'Akatsuki' and 'Kawanakajima hakuto' and of native-type peaches 'Nagano yaseito Early' and 'Noto zairaito No. 2'. FRK activity was assayed by using a reaction mixture containing either 0.5 or 50 mM fructose. Each value represents the mean of triplicate measurements and the associated SE.

Fig. 4. Changes in the fructose-6-phosphatase (Fru6Pase) activity of eating-quality peaches 'Akatsuki' and 'Kawanakajima hakuto' and of native-type peaches 'Nagano yaseito Early' and 'Noto zairaito No. 2'. Fru6Pase activity was assayed in a reaction mixture adjusted to a pH of either 5.0 or 7.2. Each value represents the mean of triplicate measurements and the associated SE.

Fig. 5. Changes in the phosphoglucose isomerase (PGI) activity of eating-quality peaches 'Akatsuki' and 'Kawanakajima hakuto' and of native-type peaches 'Nagano yaseito Early' and 'Noto zairaito No. 2'. Each value represents the mean of triplicate measurements and the associated SE.

Fig. 6. Changes in the sorbitol dehydrogenase (SDH) activity of eating-quality peaches 'Akatsuki' and 'Kawanakajimahakuto' and of native-type peaches 'Nagano yaseito Early' and 'Noto zairaito No. 2'. Each value represents the mean of triplicate measurements and the associated SE.

concentrations of either 0.5 or 50 mM (Fig. 3). FRK activity was similar for all cultivars at both concentrations, indicating that either peach fruit has both types of FRKs or that the kinetics of peach FRK is quite different from that reported for tomato. The level of FRK activity was lower for 'Noto zairaito No. 2' than for the other cultivars at all stages of fruit development, whereas that of 'Nagano yaseito Early' was higher than that of the eating-quality peach cultivars 4 months after flowering to the ripe stage.

Very little is known about plant Fru6Pase. We, therefore, measured Fru6Pase activity at two different pHs and found that it is significantly higher at pH 5.0 than at pH 7.2, although the activity patterns were similar at both pHs (Fig. 4). Fru6Pase activity was lower for 'Noto zairaito No. 2' than for the other three cultivars that exhibited similar levels of activity. Although specific hexose phosphatase has not been reported to occur in plants, it is possible that other nonspecific phosphatases could affect the hexose phosphate concentration. However, it is unclear whether the Fru6Pase activities measured in this study resulted from the activity of specific phosphatases.

PGI activity was much higher than those of other enzymes in the 4 cultivars investigated (Fig. 5). PGI activity in ripe fruits was 10 or more times greater than that of the other three enzymes.

In all cultivars, SDH activity increased as the fruit ripened (Fig. 6) which agrees with the findings of Yamada et al. (2001), who measured SDH activity and protein concentrations in the eating-quality peach 'Showahakuto'. The activity of SDH was significantly higher in the eating-quality peach cultivars than in the native-type peach cultivars at all developmental stages tested in this study.

Fig. 7. Hexose phosphate content in the fruit of different peach cultivars. Fructose-6-phosphate (Fru6P) and glucose-6-phosphate (Glc6P) concentrations were measured in the fruit of eating-quality peaches 'Akatsuki' and 'Kawanakajimahakuto' and of native-type peaches 'Nagano yaseito Early' and 'Noto zairaito No. 2' at 3 months after flowering. Each value represents the mean of triplicate measurements and the associated SE.

Hexose-phosphate content

The low fructose content in native-type peaches may possibly be explained by the rapid conversion of fructose to Fru6P. If so, the levels of Fru6P and Glc6P, which are produced from Fru6P by PGI, would be higher in native-type cultivars than in eating-quality ones. However, the results of our study showed that the Fru6P contents were not significantly different among the 4 cultivars ($P < 0.05$, analysis of variance; Fig. 7). The Glc6P contents in the native-type peach cultivars were intermediate between 'Kawanakajimahakuto' and 'Akatsuki'.

Discussion

Clear differences in the fructose contents of eating-quality peaches and native-type peaches have been described previously by Moriguchi et al. (1990a). The enzymes FRK, Fru6Pase, and SDH can affect the concentration of fructose in the fruit because fructose acts as either the enzyme product or the substrate for these enzymes (Fig. 1). PGI catalyzes the inter-conversion between Fru6P and Glc6P, which can affect the ratio of fructose to glucose. Our assays on the activities of these fructose-related enzymes in the eating-quality and native-type peach cultivars showed that SDH activity levels differed significantly between the two groups. This finding indicates that differences in the capacity for fructose formation by SDH may be an important factor that affects the concentration of fructose in peach fruit.

SDH has been purified from Japanese pear fruit with the use of sodium dodecyl sulfate polyacrylamide gel electrophoresis (Oura et al., 2000). The K_m values

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obtained for sorbitol and fructose for Japanese pear SDH are 96 mM and 4240 mM, respectively, an indication that SDH catalyzes the oxidation of sorbitol to fructose in vivo. Therefore, the high SDH activity exhibited by the eating-quality peach cultivars most likely contributes to their higher fructose level.

If the high concentration of fructose in the eating-quality peach cultivars was not related to the greater capacity for fructose formation, but to a low capacity for converting the fructose to Fru6P, we would have expected the Fru6P content to be relatively low in the eating-quality peach cultivars (Fig. 1). Indeed, a reduction in the activity of FRK, which results in a decrease in the conversion rate of fructose to Fru6P, is known to cause a decrease in the Fru6P content and a subsequent increase in the fructose content in tomato fruit (Dai et al., 2002). However, the concentrations of Fru6P measured were not lower in the eating-quality peach cultivars than in the native-type peaches. This suggests that the high concentrations of fructose found in the eating-quality cultivars are related to fructose formation rather than to the conversion of fructose to Fru6P.

The activity of FRK, the enzyme that phosphorylates fructose to produce Fru6P, in 'Nagano yaseito Early' surpassed that of the eating-quality cultivars between 4 months after flowering and harvest, but was similar to the others at 3 months after flowering. At the early developmental stage, the fructose content differed between the two groups. In addition, the level of FRK activity for 'Noto zairaito No. 2' was lower than that for the eating-quality peach cultivars at all stages tested in this study. It is, therefore, unlikely that FRK regulates the concentration of fructose in any of the 4 peach cultivars investigated.

The ratio of Glc6P to Fru6P is affected in a *Clarkia* mutant that displays decreased PGI activity (Kruckeberg et al., 1989). Low PGI activity may affect the concentration of fructose by influencing the Glc6P/Fru6P ratio, but our data show no clear differences in PGI activity between the two groups. In addition, the activity of PGI was higher than that of the other enzymes, indicating that the isomerization by PGI is not a rate-limiting step. Schaffer et al. (1999) also concluded that PGI is unlikely to affect the sugar composition of fruit.

The sucrose content that was found to be higher in the eating-quality peach cultivars than in the native-type peach cultivars may be attributed to a type of sucrose synthase, which catalyzes the production of sucrose. This enzyme plays a key role in sucrose accumulation in ripe peach fruit (Moriguchi et al., 1990b). Fructose is an important substrate for sucrose synthesis. If sucrose synthase metabolized fructose, the latter would be consumed more rapidly in eating-quality peach cultivars, which are characterized by higher sucrose concentrations than are native-type peach cultivars (Fig. 1). Moriguchi et al. (1991) reported that sucrose synthase activity in ripe fruit of 'Akatsuki' was higher than in

fruits of 'Nagano yaseito Early' of comparable ripeness. However, the fructose content in the eating-quality peach cultivars was also relatively high. Much evidence suggests that sucrose concentrations are not directly related to fructose concentrations; however, more detailed analyses will be needed with regard to the properties and the activities of sucrose-related enzymes in all of the 4 cultivars we investigated.

Many investigations on sugar composition of fruit have mainly focused so far on sucrose, but they also provided useful information to understand the regulatory mechanism of fructose content by analogy. A low sucrose content in cultivated tomatoes is caused by an increased activity of an enzyme known as acid-invertase (Schaffer et al., 1999). Sucrose accumulation in the mature fruit of the Japanese pear results from an increase in the concentration of non-phosphorylated sucrose synthase, an enzyme that is involved in sucrose synthesis rather than in sucrose cleavage (Tanase et al., 2002). On the basis of these findings, it seems likely that the main determining factors of sucrose concentrations are the enzymes involved either directly in sucrose formation or in its conversion to other metabolites. With respect to acid-invertase, which catalyzes the conversion of sucrose to glucose and fructose, the concentrations of glucose and fructose are higher when the sucrose content is low in the cultivated tomatoes (Schaffer et al., 1999). In this study, the content of Fru6P, which is the product of fructose metabolism, was similar for eating-quality peach cultivars and for native-type cultivars. Furthermore, no clear differences in FRK and Fru6Pase activities were observed between the two groups. Based on fructose formation between the two groups of peaches, it seems that the regulation of fructose level is related to SDH.

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モモの生食用品種と在来品種の果実におけるフルクトース含量とフルクトース関連酵素活性

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摘 要

モモの生食用品種および在来品種の果実におけるフルクトース含量には明らかな差異がみられる。そこで、モモ果実においてフルクトース含量を制御する要因を明らかにするため、生食用品種の「あかつき」と「川中島白桃」、および在来品種の「長野野生桃早生」と「能登在来桃 No. 2」におけるフルクトース関連酵素の活性を測定した。生食用品種の果実におけるフルクトース含量は、開花3ヶ月後から成熟期にかけて7から12 mg・g⁻¹FWの間を推移した。在来品種の果実におけるフルクトース含量は極めて低く、1 mg・g⁻¹FW以下であった。果実におけるフルクトキナーゼ、フルクトース6リン酸ホスファターゼおよびホスホグルコースイソメラーゼ(PGI)の活性については、「能登在来桃 No. 2」で低かったものの、生食用品種と在来品種の間での明確な差は認められなかった。またすべての品種の果実において、

PGI活性は他の酵素の活性とくらべて非常に高かったことから、PGIの反応はフルクトース合成の律速段階ではないと考えられた。さらに果実におけるフルクトース6リン酸含量についても、生食用品種と在来品種の間で明確な差は認められなかった。これらの結果から、両品種間におけるフルクトース含量の差異は、フルクトースをフルクトース6リン酸、さらにはグルコース6リン酸に変換する能力の違いではなく、フルクトース合成能の違いに由来することが示唆された。実際、NAD依存性ソルビトール脱水素酵素(SDH)活性は果実の成長期間を通して生食用品種において在来品種より高かった。したがって、ソルビトールからフルクトースの合成に寄与するSDHがモモ果実のフルクトース含量の調節に関与することが示唆された。