

Article

Dynamic Analysis of Sugar, Organic Acid, Phytohormones, and Enzyme Activities in Developing Fruit of White- and Red-Fleshed Loquat (*Eriobotrya japonica* Lindl.)

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Highlights

What are the main findings?

- Total sugar contents significantly increase during loquat fruit development.
- Fructose, glucose, and sucrose were the major sugars in loquat fruit, and the major organic acid was malic acid.
- The enzymes of SS, SPS and PFK play vital roles in sugar accumulation, and the activities of PEPC, NADP-ME, NAD-ME were crucial for organic acid metabolism.
- IAA and GA3 play key roles in fruit enlargement, while ABA is important for fruit ripening in loquats.

What are the implications of the main findings?

- The findings advance the understanding of the physiological basis of loquat quality formation.
- The findings provide a theoretical foundation for breeding high-sugar, high-quality loquat cultivars.

Abstract

Sweet and sour flavors are the most important indicators of loquat fruit quality; they are determined not only by variety but also by the flesh type and the concentration and change patterns of sugars, organic acids, related enzyme activities, and endogenous phytohormones. This study aimed to comprehensively evaluate the physiological and biochemical characteristics associated with loquat fruit flavor formation by analyzing the changes and correlation in sugars, organic acids, enzyme activities, and endogenous hormones during fruit development in the white-fleshed, high-sugar cultivar ‘Qixing’ and the red-fleshed, sour-sweet cultivar ‘Huoju’. The results indicated a significant increase in total soluble sugars and individual sugars (mainly fructose, glucose, and sucrose), and a sharp decrease in organic acids (mainly malic acid). Correlation analysis revealed that the activities of sucrose synthase (SS), sucrose phosphate synthase (SPS), and phosphofructokinase (PFK) were positively associated with sugar accumulation. In contrast, phosphoenolpyruvate carboxylase (PEPC), NADP-malic enzyme (NADP-ME), and NAD-malate dehydrogenase (NAD-MDH) were crucial for organic acid metabolism.

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Phytohormone analysis indicated that indole-3-acetic acid (IAA) and gibberellic acid (GA3) play vital roles in fruit enlargement, while abscisic acid (ABA) is important for fruit ripening in loquats. These findings provide insights into the physiological mechanisms underlying loquat fruit quality formation, reveal the enzymatic or hormonal regulatory effects on sugar accumulation and acid degradation, and provide a theoretical basis for improving the fruit flavor quality.

Keywords: *Eriobotrya japonica* Lindl.; fruit development; sugar; organic acid; phytohormone

1. Introduction

Loquat (*Eriobotrya japonica* Lindl.) is a subtropical, evergreen fruit tree belonging to the Rosaceae family, originating from Southwest China [1–3]. It is well known for its tender, juicy flesh and delicious flavor; it is also rich in vitamins, minerals, and various bio-active substances [4–6]. The health benefits of loquat include eliminating phlegm, relieving coughs, moistening the lungs, stimulating saliva production and appetite, and aiding digestion [7–9]. The quality of loquats, especially their sweet and sour flavors, is a key factor determining their commercial value and consumer acceptance [10]. Flavor formation in loquat depends not only on the variety but also on the levels, composition ratios, and dynamic changes in sugar and organic acids in the fruits [11]. Therefore, analyzing the physiological mechanisms of sugar accumulation, organic acid metabolism, and related enzyme activities during loquat fruit development is of great theoretical and practical significance for quality regulation and genetic improvement.

Generally, loquats are divided into white- and red-fleshed (also known as yellow-fleshed) types based on their flesh color. White-fleshed loquats usually have a more delicious taste and higher nutritional value than red-fleshed types, which are characterized by high yields and suitability for long-distance transportation and are therefore widely cultivated in China [12,13]. Soluble sugars and organic acids are the main substances that influence fruit taste and flavor and play a significant role in fruit quality [10]. Sucrose, glucose, and fructose are the major soluble sugars found in loquat fruit, with sucrose often regarded as a key contributor to sweetness [14,15]. Several key enzymes regulate sucrose accumulation; for instance, sucrose synthase (SS) and sucrose phosphate synthase (SPS) catalyze sucrose synthesis, and their activities are positively correlated with sucrose accumulation rate [16,17]. Moreover, phosphofructokinase (PFK) is the first rate-limiting enzyme of the glycolytic pathway, irreversibly catalyzing the conversion of fructose-6-phosphate to fructose-1,6-bisphosphate, and thus it occupies a central hub position in the sugar metabolic network. During fruit development, glycolytic flux not only provides the requisite ATP for cell division and expansion but also supplies carbon skeletons for secondary metabolite biosynthesis via branching points such as the pentose phosphate pathway. More importantly, PFK activity directly influences the downstream partitioning of glycolytic carbon, thereby regulating the accumulation ratio of hexoses (glucose and fructose) to sucrose in the fruit. This ratio serves as a critical chemical basis for determining fruit sweetness, flavor, and overall organoleptic quality. Therefore, an in-depth investigation into the biological functions of PFK at specific stages of fruit development holds great scientific significance for elucidating the metabolic regulatory mechanisms underlying fruit quality formation. However, research on sugar-accumulation patterns in loquat fruits and their correlation with changes in key enzyme activities remains limited, highlighting the need for further in-depth exploration. Organic acids profoundly influence the flavor of loquat fruit [18]. The organic acids in loquat fruit are mainly malic, citric, and

quinic acids [19]. Organic acids accumulate during early fruit development, but they decrease during fruit ripening, as they are consumed through respiration or used as precursors for the synthesis of other substances [20–22]. The biosynthesis and degradation of organic acids are regulated by key enzymes, including phosphoenolpyruvate carboxylase (PEPC), NAD-malate dehydrogenase (NAD-MDH), and NADP-malic enzyme (NADP-ME) [23,24]. Clarifying the dynamic activities of these enzymes at different stages of fruit development is crucial for understanding the metabolic patterns of organic acids in loquats. However, systematic research on the coordinated changes in sugar and acid metabolism throughout the entire developmental period, as well as the mechanisms driving key enzyme activities, is lacking.

Phytohormones act as endogenous signaling molecules that play critical regulatory roles in fruit development, ripening, and quality formation [25]. To comprehensively elucidate the hormonal regulatory network governing sugar and organic acid metabolism in fruits, the present study selected four representative phytohormones—auxin (IAA), abscisic acid (ABA), gibberellic acid (GA₃), and zeatin—for concurrent analysis. IAA primarily regulates early fruit development by promoting cell division and expansion [26]. ABA serves as a central regulator of fruit ripening, significantly promoting the accumulation of glucose and fructose, while modulating organic acid metabolism through the regulation of key genes such as *ABF2*, *PEPC*, and *CS* [27–29]. GA₃ plays vital roles in fruit set, cell elongation, and sink strength establishment, with demonstrated effects on soluble sugar content and organic acid composition [30]. Zeatin, a major bioactive cytokinin, promotes cell proliferation and fruit enlargement, and its endogenous levels have been positively correlated with soluble sugar accumulation and sink activity [31]. These four phytohormones act at distinct developmental stages and physiological processes, forming a complex synergistic and antagonistic network that collectively regulates the metabolic balance of sugars and organic acids in fruits. Therefore, the simultaneous analysis of these four hormones in the present study is designed to systematically unravel the synergistic regulatory mechanisms of hormonal signaling in fruit quality formation, thereby providing a theoretical foundation for fruit quality improvement. The objective of this study was to analyze dynamic changes in the contents of soluble sugars (sucrose, glucose, fructose, and sorbitol) and organic acids (malic, citric, and quinic acids), as well as the activities of sugar-related enzymes (SS, SPS, and PFK) and key enzymes for organic acid metabolism (PEPC, NAD-MDH, and NADP-ME) at different developmental stages of loquat fruits. Two different types of loquat cultivars were used: the white-fleshed, high-sugar cultivar ‘Qixing’; and the red-fleshed, sour-sweet cultivar ‘Huoju’. The relationships between sugars, organic acids, and enzyme activities were also assessed. Furthermore, the levels of major endogenous phytohormones, including indole-3-acetic acid (IAA), abscisic acid (ABA), gibberellic acid (GA₃), and zeatin, were dynamically evaluated during fruit development. These findings provide insights into the physiological basis of loquat fruit quality, reveal the enzymatic or hormonal regulatory effects on sugar accumulation and acid degradation, and provide a theoretical basis for improving the fruit flavor quality.

2. Materials and Methods

2.1. Plant Materials and Experimental Design

In this study, 7-year-old trees of two loquat cultivars with different flesh types, both bred by the Shanghai Academy of Agricultural Sciences (SAAS), were used. The cultivars included the white-fleshed, high-sugar cultivar ‘Qixing’ and the red-fleshed, sour-sweet cultivar ‘Huoju’. Both cultivars had the same maturity period, both ripening in mid-May under greenhouse conditions in Shanghai. All the trees were planted in a greenhouse at the Zhuang-hang Comprehensive Experimental Station of SAAS, Shanghai, China, with a spacing of 3 × 4 m. They received the same field management practices for disease and

pest control. Disease-free loquat fruits of uniform size were randomly collected from each cultivar at six distinct developmental stages (Figure 1): small green fruits with a diameter of approximately 1–2 cm (S1; 1 March 2024), enlarged green fruits with a diameter of approximately 2–3 cm (S2; 27 March 2024), fruits in the color-transition stage with half green and half yellow (S3; 22 April 2024), unripe fruits after color change (S4; 30 April 2024), ripe fruits (S5; 7 May 2024), and fully ripe fruits (S6; 16 May 2024). When sampling, a total of 30 fruits of uniform size and free from visible defects were randomly collected and were divided into two portions: one portion was immediately used for physicochemical parameters analyses, including weight, diameter, firmness, and total soluble solids, which were measured in a subset of the fruits ($n = 10$). The other portion was snap-frozen in liquid nitrogen; ground into powder; and then stored at $-80\text{ }^{\circ}\text{C}$ for subsequent analyses, including assessments of sugars, organic acids, plant hormones, and enzyme activities. Each measurement (cultivar $\times$ developmental stage) consisted of three independent biological replicates ($n = 3$), yielding a total of 36 independent samples, i.e., 2 cultivars $\times$ 6 stages $\times$ 3 replicates.

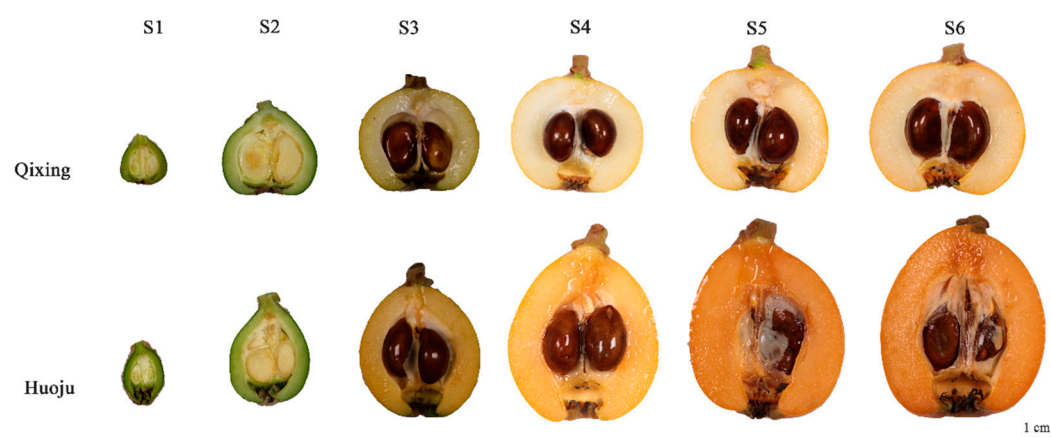


Figure 1. Phenotypes of loquat fruits at six developmental stages in ‘Qixing’ and ‘Huoju’. Scale bar = 1 cm.

2.2. Physicochemical Properties Analysis of Loquat Fruit

The fruits collected at each developmental stage were assessed for various characteristics, including weight, transverse and longitudinal diameters, firmness, total soluble solids (TSS), titratable acidity (TA), individual sugars (fructose, sucrose, glucose, and sorbitol), organic acids (quinic, citric, and malic acids), and sugar- or acid-related enzyme activities. Fruit weight and diameter were measured using an electronic scale (g) and a digital caliper (mm), respectively. TSS was evaluated using a handheld PAL-1 palette refractometer (ATAGO Co., Ltd., Tokyo, Japan), while TA was measured by titration, with 0.01 M NaOH and 0.1% phenolphthalein as indicators; both results were expressed as percentages (%).

2.3. Determination of Sugars, Organic Acids, and the Activities of Sugar- and Acid-Related Enzymes in Loquat Fruits

Individual sugars and organic acids were extracted from 1 g of powder sample using 3 mL of 80% ethanol at $37\text{ }^{\circ}\text{C}$ for 30 min. The mixture was then centrifuged at 4000 rpm for 10 min, and the residue was re-extracted twice following the same procedure. The supernatants from the three extractions were mixed and adjusted to a final volume of 10 mL. Subsequently, 1 mL of each extract was evaporated under vacuum at $25\text{ }^{\circ}\text{C}$, re-dissolved in 1 mL of double-distilled water (ddH₂O), and filtered through a $0.22\text{ }\mu\text{m}$ Millipore filter. The soluble sugar and organic acid concentrations were analyzed using a high-

performance liquid chromatography (HPLC) system (Waters e2695 Separations Module; Waters, Milford, MA, USA) according to the method described in the reported literature [32]. The sugar composition determination was carried out using a CARBOsep CHO-620 Ca-type sugar column (6.5 * 300 mm, 10 μ m) at a column temperature of 90 °C. The mobile phase was ultra-pure water, the flow rate was 0.5 mL/min, and the detector was a Waters 2414, which was used to detect the soluble sugar concentration; the injection volume was 10 μ L. The acid component determination was carried using a C18-WP HPLC column (4.6 * 250 mm, 5 μ m). The mobile phase was 0.2% phosphoric acid with a flow rate of 0.5 mL/min and a column temperature of 37 °C, and the injection volume was 10 μ L. The standards of sugar and acid were chromatographically pure sucrose (cas: 57-50-1), glucose (cas: 50-99-7), fructose (cas: 57-48-7), sorbitol (cas: 50-70-4), quinic acid (cas: 77-95-2), malic acid (cas: 97-67-6), and citric acid (cas: 77-92-9) purchased from Sigma-Aldrich (Shanghai) Trading Co. Ltd. (Shanghai, China). The activities of enzymes involved in fruit sugar and organic acid biosynthesis and degradation, including phosphofructokinase (PFK), sucrose phosphate synthase (SPS), sucrose synthase (SS), phosphoenolpyruvate carboxylase (PEPC), NAD-malate dehydrogenase (NAD-MDH), and NADP-malic enzyme (NADP-ME), were quantified using appropriate detection kits (Sangon Biotech, Shanghai, China) in accordance with the manufacturer's instructions. Specifically, PFK was determined using PFK Activity Assay Kit (Catalog No. D799442, Sangon Biotech), SPS was determined using SPS Activity Assay Kit (Catalog No. D799788, Sangon Biotech), SS was determined using SS Activity Assay Kit (Catalog No. D799786, Sangon Biotech), PEPC was determined using PEPC Activity Assay Kit (Catalog No. D799448, Sangon Biotech), NAD-MDH was determined using NAD-MDH Activity Assay Kit (Catalog No. D799214, Sangon Biotech), and NADP-ME was determined using NADP-ME Activity Assay Kit (Catalog No. D799254, Sangon Biotech). The detailed methodology, including the assay principle, reaction conditions, and calculation of enzyme activity, can be found in the corresponding kits mentioned above. The results were expressed as U g⁻¹ FW. All indicators were measured in triplicate.

2.4. Determination of Endogenous Plant Hormones in Loquat Fruits

Approximately 0.5 g of fresh tissue from each developmental stage was ground in liquid nitrogen and digested in 5 mL ethyl acetate for 12 h at 4 °C. The mixture was then centrifuged at 10,000 rpm at 4 °C for 10 min; the residue was further digested in 3 mL ethyl acetate and centrifuged at 10,000 rpm at 4 °C for 10 min. The supernatant was dried under nitrogen flow at 25 °C, then dissolved in 300 μ L chromatographic methanol, and subsequently subjected to ultrasonic extraction for 10 min. Finally, the solution was filtered through 0.22 μ m membrane filters, and 5 μ L was injected for analysis. The levels of endogenous plant hormones (IAA, ABA, GA3, and zeatin) were analyzed using liquid chromatography–mass spectrometry (LC-MS) based on the method described in our previously published work [33]. An Acquity UPLC system (Waters Corp., Milford, MA, USA) and an AB SCIEX QTRAP® 5500 mass spectrometer (AB SCIEX, Framingham, MA, USA) were interconnected to acquire phytohormone quantitative data using the Analyst 1.6 software (AB SCIEX, Framingham, MA, USA) equipped with an ESI Turbo Ion-Spray interface. The column was an Acquity® BEH C18 column (100 mm * 2.1 mm, 1.8 μ m, Waters). The following ion source parameters were applied: source temperature, 550 °C; Ion-Spray voltage, –4500 V; Ion Source Gas 1, 55 psi; and Ion Source Gas 2, 55 psi. The mobile phase, consisting of acetonitrile (solvent A) and 0.02% (v/v) glacial acetic acid in water (solvent B), was pumped at a flow rate of 0.15 mL min⁻¹, with a volume ratio (A:B) of 60:40. The injection volume was 2 μ L at a column temperature of 30 °C, and it was separated for 7 min. Standards for IAA (cas:87-51-4, Sigma-Aldrich, Shanghai China), ABA (cas:21293-29-8, Sigma-Aldrich, Shanghai, China), GA3 (cas:77-06-5, Sigma-Aldrich, Shanghai, China),

and zeatin (cas:13114-27-7, Sigma-Aldrich, Shanghai, China) were used to optimize the mass spectrometric parameters and fragment spectra. Calibration curves for IAA, ABA, GA3, and zeatin standards were obtained at eight different concentrations (0, 1.5625, 3.125, 6.25, 12.5, 25, 50, and 100 ng/mL). All samples were analyzed with three biological replicates, and results were expressed as means $\pm$ standard deviation (SD).

2.5. Statistical Analysis

Our study included two experimental factors: variety (two cultivars) and developmental stages (six stages: S1–S6). Based on the biological questions we aimed to address, these two factors were analyzed separately. Specifically, (1) to evaluate the effect of developmental stage, a one-way ANOVA analysis in SPSS software (version 18.0; SPSS Inc., Chicago, IL, USA) was performed for each variety independently, comparing the six developmental stages within each cultivar, and significant differences were compared using Duncan's test; and (2) to evaluate the effect of variety, a t-test analysis was performed at each developmental stage independently, comparing the two cultivars at the same stage. Differences at $p \leq 0.05$ were considered statistically significant. Correlation analysis was also performed using SPSS, Spearman's rank correlation coefficient was employed to evaluate the relationships, and a two-tailed p -value < 0.05 was considered statistically significant. The strength of the correlations was interpreted based on the absolute r -value, where $|r| \geq 0.7$ indicated a very strong correlation, $0.5 \leq |r| < 0.7$ indicated a strong correlation, $0.3 \leq |r| < 0.5$ indicated a moderate correlation, and $|r| < 0.3$ indicated a weak correlation. Graphics were created using GraphPad Prism 6.0 (GraphPad Software, Inc., San Diego, CA, USA).

3. Results

3.1. Physicochemical Properties of 'Qixing' and 'Huoju' During Loquat Fruit Development

Physicochemical properties, including fruit weight, fruit diameter, fruit firmness, total soluble solids (TSS), titratable acidity (TA), and TSS-TA ratio, were significantly different ($p < 0.05$) across the developmental stages (Table 1). For 'Qixing', fruit weight increased significantly with developmental stage, peaking at S6 at 45.9 g, approximately 16.68-fold greater than at S1 (2.6 g). The changes in fruit diameter were similar to those in fruit weight, reaching their maximum at S6, with both transverse and longitudinal diameters being 2.55-fold greater at S6 than at S1 (Table 1). There was no obvious difference detected in fruit shape index (Table 1). Fruit firmness significantly declined during development by 6.86-fold, from 10.1 N kg⁻¹ at S1 to 1.5 N kg⁻¹ at S6 (Table 1). The TSS content and TSS-TA ratio increased significantly, reaching their maximum values of 16.5 and 30.7, respectively, in S6 (Table 1). In contrast, the TA content displayed a 2.1-fold decrease from 1.1% in S1 to 0.5% in S6 (Table 1). In 'Huoju', all physicochemical properties showed a changing pattern similar to that of 'Qixing' (Table 1).

Table 1. Fruit physicochemical properties of 'Qixing' and 'Huoju' at six developmental stages.

Developmental Stage	'Qixing'						'Huoju'					
	S1	S2	S3	S4	S5	S6	S1	S2	S3	S4	S5	S6
Fruit weight (g)	2.8 $\pm$ 0.10 f	8.7 $\pm$ 0.28 e	29.2 $\pm$ 0.46 d	37.5 $\pm$ 1.28 c	41.7 $\pm$ 1.29 b	45.9 $\pm$ 1.10 a	2.8 $\pm$ 0.11 e	8.9 $\pm$ 0.17 d	31.6 $\pm$ 1.95 c	47.4 $\pm$ 1.41 b	44.6 $\pm$ 1.39 b	59.4 $\pm$ 1.56 a
WD (mm)	17.7 $\pm$ 0.28 f	26.1 $\pm$ 0.36 e	38.3 $\pm$ 0.24 d	40.8 $\pm$ 0.54 c	43.1 $\pm$ 0.52 b	45.1 $\pm$ 0.52 a	16.6 $\pm$ 0.17 e	23.8 $\pm$ 0.24 d	36.6 $\pm$ 0.58 c	42.3 $\pm$ 0.39 b	41.7 $\pm$ 0.79 b	45.1 $\pm$ 0.58 a
LD (mm)	16.2 $\pm$ 0.22 e	22.3 $\pm$ 0.36 d	35.2 $\pm$ 0.74 c	38.1 $\pm$ 0.99 b	38.7 $\pm$ 0.76 b	41.2 $\pm$ 0.69 a	21.3 $\pm$ 0.38 e	29.5 $\pm$ 0.52 d	44.9 $\pm$ 1.19 c	49.1 $\pm$ 1.46 b	44.5 $\pm$ 0.62 c	55.4 $\pm$ 0.78 a
Fruit shape index	0.9 $\pm$ 0.01 a	0.9 $\pm$ 0.02 b	0.9 $\pm$ 0.02 a	0.9 $\pm$ 0.03 a	0.9 $\pm$ 0.02 ab	0.9 $\pm$ 0.01 a	1.3 $\pm$ 0.02 a	1.3 $\pm$ 0.02 ab	1.2 $\pm$ 0.03 ab	1.2 $\pm$ 0.03 b	1.1 $\pm$ 0.03 c	1.2 $\pm$ 0.03 ab
Fruit firmness (N kg ⁻¹)	10.1 $\pm$ 0.14 a	9.6 $\pm$ 0.33 a	2.1 $\pm$ 0.09 b	1.7 $\pm$ 0.12 bc	1.5 $\pm$ 0.05 c	1.5 $\pm$ 0.11 c	9.8 $\pm$ 0.24 b	11.0 $\pm$ 0.37 a	2.7 $\pm$ 0.14 c	1.6 $\pm$ 0.07 d	1.4 $\pm$ 0.06 d	1.6 $\pm$ 0.08 d

TSS (%)	10.5 ± 0.24 c	8.6 ± 0.22 d	8.5 ± 0.22 d	12.4 ± 0.18 b	13.3 ± 0.32 b	16.5 ± 0.61 a	10.7 ± 0.55 b	9.5 ± 0.23 c	8.0 ± 0.56 d	10.5 ± 0.89 b	10.2 ± 0.21 bc	12.1 ± 0.34 a
TA (%)	1.1 ± 0.09 b	1.8 ± 0.01 a	1.3 ± 0.09 b	0.6 ± 0.05 c	0.5 ± 0.06 c	0.5 ± 0.03 c	1.0 ± 0.08 b	1.4 ± 0.03 a	1.2 ± 0.03 a	0.6 ± 0.14 c	0.4 ± 0.42 d	0.5 ± 0.29 d
TSS/TA	9.4 ± 0.93 d	5.1 ± 0.15 d	6.5 ± 0.55 d	19.9 ± 1.78 c	29.0 ± 3.94 a	30.7 ± 3.23 a	11.1 ± 0.92 c	7.0 ± 0.19 d	6.5 ± 0.18 d	17.7 ± 0.28 b	25.2 ± 3.01 a	28.3 ± 0.30 a

Notes: WD, wide diameter; LD, longitudinal diameter. Fruit shape index was calculated as the ratio of LD to WD, and the data are expressed as the mean ± standard deviation (n = 3). Different lower-case letters in each row indicate significance at $p < 0.05$.

3.2. Individual Sugars and Organic Acid Levels of ‘Qixing’ and ‘Huoju’ During Loquat Fruit Development

The changes in sugar concentrations during fruit development were similar in white-fleshed ‘Qixing’ and red-fleshed ‘Huoju’ (Figure 2). Fructose, glucose, and sucrose were the major sugars detected and increased continuously throughout the developmental stages; sorbitol was significantly high in the green-fruit stages (S1–S2), declined sharply and significantly at the color-transition stage (S3), and then remained low and stable during S3 to S6. Fructose concentrations were at relatively low levels before S3; increased from S1 to S6 sharply by 5.80- and 3.66-fold; and finally peaked at S6, with a value of 26.17 and 17.41 mg g^{−1} FW in ‘Qixing’ and ‘Huoju’, respectively (Figure 2a). The fructose content in ‘Qixing’ was always higher than that in ‘Huoju’, especially during the later stages of fruit development (S3–S6), and differences in the fructose content between ‘Qixing’ and ‘Huoju’ during S3–S6 were significant (Figure 2a). Glucose concentration increased steadily from S1 to S6 by 7.19- and 5.39-fold and reached 12.44 and 15.04 mg g^{−1} FW in ‘Qixing’ and ‘Huoju’, respectively (Figure 2b). The glucose content in ‘Huoju’ was always higher than that in ‘Qixing’, and except for S4, the glucose levels in ‘Huoju’ during other five developmental stages are significantly higher than those in ‘Qixing’ (Figure 2b). Sucrose concentration followed a similar pattern to that of fructose: sucrose content was extremely low during the green-fruit stages (S1–S2), increased rapidly from S3, and peaked at S5 in ‘Qixing’ (69.84 mg g^{−1} FW) and at S4 in ‘Huoju’ (45.35 mg g^{−1} FW), respectively; it then decreased slightly when the fruits ripened (Figure 2c). The sucrose content in ‘Qixing’ remained higher than that in ‘Huoju’, especially during the later stages of fruit development (S4–S6), and differences in the sucrose content between ‘Qixing’ and ‘Huoju’ during S4–S6 were significant (Figure 2c). The levels of sorbitol both in ‘Qixing’ and ‘Huoju’ were significantly the highest in the green-fruit stage, S1 (12.58 and 11.76 mg g^{−1} FW in ‘Qixing’ and ‘Huoju’, respectively); exhibited a marked decrease by 3.89- and 3.81-fold from S2 to S3; and remained basically the same during later developmental stages (S3–S6). No significant differences were found in sorbitol between ‘Qixing’ and ‘Huoju’ (Figure 2d).

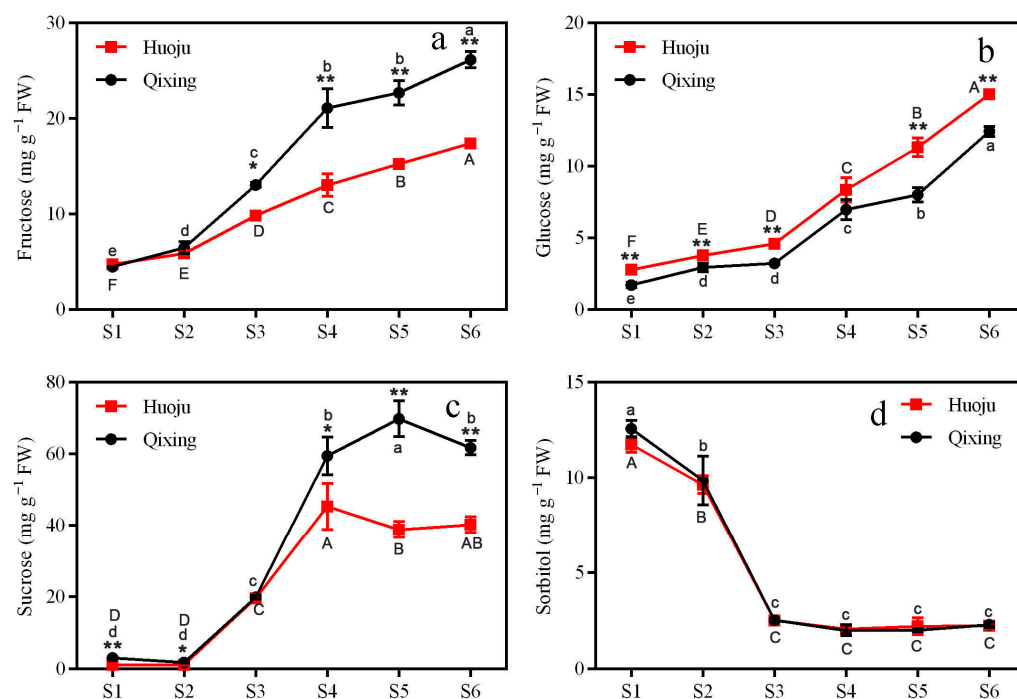


Figure 2. Changes in fructose (a), glucose (b), sucrose (c), and sorbitol (d) of 'Qixing' and 'Huoju' fruits at six developmental stages. Bars indicate standard error (n = 3). One asterisk (*) indicates the significance of each developmental stage between two cultivars based on t-test at $p < 0.05$; two asterisks (**) indicate the significance of each developmental stage between two cultivars based on t-test at $p < 0.01$. Different lowercase letters indicate the significance of six developmental stages of 'Qixing' based on Duncan's test at $p < 0.05$. Different capital letters indicate the significance of six developmental stages of 'Huoju' based on Duncan's test at $p < 0.05$.

Before analyzing the trends of organic acids, the dynamic change curves of TA in 'Qixing' and 'Huoju' were plotted. They revealed that the change in TA was similar in both cultivars, and they exhibited an inverted V-shaped trend (Figure 3a). The level of TA before S3 both in 'Qixing' and 'Huoju' was significantly higher than that during S4–S6 (Figure 3a). Quinic, malic, and citric acids were the major organic acids detected in the loquat fruits, with malic and quinic acids predominant throughout fruit development (Figure 3). Changes in citric acid concentration were similar between 'Qixing' and 'Huoju'. It was low at S1 (0.15 and 0.64 mg g⁻¹ FW in 'Qixing' and 'Huoju', respectively), increased significantly and peaked at S2 (0.27 and 1.18 mg g⁻¹ FW, respectively) by about 1.8-fold from S1 to S2, and then decreased sharply and stabilized at a relatively low level as fruit developing S3–S6 (Figure 3b). Citric acid concentration in green fruit (S1–S2) of 'Huoju' was significantly higher than that of 'Qixing' (Figure 3b). Changes in malic acid concentration were also similar between 'Qixing' and 'Huoju'. It increased significantly in early fruit developmental stages (S1–S3), and the difference in malic acid between 'Qixing' and 'Huoju' was significant during S1–S3 (Figure 3c). Malic acid content peaked at S2 (19.61 mg g⁻¹ FW) in 'Qixing' and at S3 (19.37 mg g⁻¹ FW) in 'Huoju', and then declined significantly and sharply as the maturity of fruits in later development (S4–S6) (Figure 3c). The change in malic acid content (Figure 3c) followed a pattern similar to that of TA (Figure 3a). Quinic acid was highest at S1 (27.85 and 22.30 mg g⁻¹ FW in 'Qixing' and 'Huoju', respectively) and decreased continuously and significantly, with a sharp decline from S2 to S3 by 3.07- and 4.29-fold in 'Qixing' and 'Huoju', respectively, and then remained stable in later developmental stages (S3–S6) (Figure 3d).

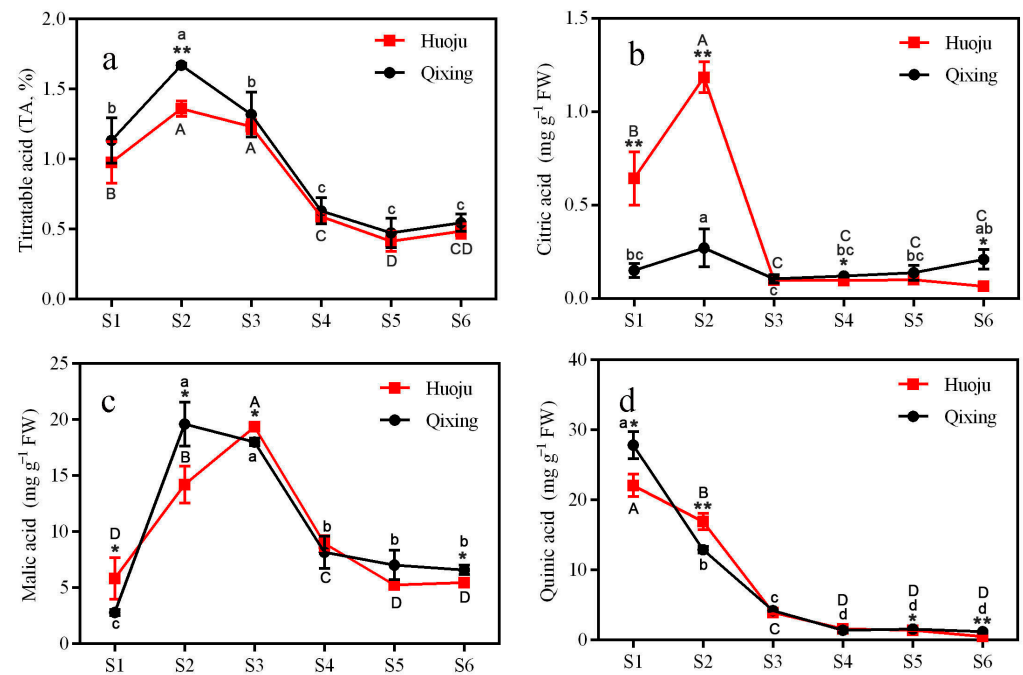


Figure 3. Changes in TA (a), citric acid (b), malic acid (c), and quinic acid (d) in 'Qixing' and 'Huoju' fruits at six developmental stages. Bars indicate standard error (n = 3). One asterisk (*) indicates the significance of each developmental stage between two cultivars based on t-test at $p < 0.05$; two asterisks (**) indicate the significance of each developmental stage between two cultivars based on t-test at $p < 0.01$. Different lowercase letters indicate the significance of six developmental stages of 'Qixing' based on Duncan's test at $p < 0.05$. Different capital letters indicate the significance of six developmental stages of 'Huoju' based on Duncan's test at $p < 0.05$.

3.3. Changes in Sugar- and Organic Acid-Related Enzyme Activities During Fruit Development

SS activity increased slightly at S2, then increased significantly, peaked at S4 (341.95 U g⁻¹ FW) of 'Huoju' and at S5 (350.82 U g⁻¹ FW) of 'Qixing', and then decreased as the fruit developed (Figure 4a). Overall, the SS activity in 'Huoju' was higher than that in 'Qixing' during early developmental stages (S1–S4), but during later developmental stages (S5–S6, i.e., fruit-ripening stages), 'Qixing' showed higher activity (Figure 4a). No significant differences in SS activity were detected between 'Qixing' and 'Huoju' at the same developmental stage (Figure 4a). The SPS activity increased gradually and peaked at S4 (809.97 and 406.23 U g⁻¹ FW in 'Qixing' and 'Huoju', respectively) and then decreased as fruit developed (Figure 4b). The SPS activity in 'Qixing' was always higher than that in 'Huoju' throughout the developmental stages, especially during ripening (S4–S6) (Figure 4b). The differences in SPS activity between 'Qixing' and 'Huoju' at S2, S4, S5, and S6 were significant (Figure 4b). In 'Qixing', the PFK activity decreased slightly before fruit transitioning (S3) and then increased gradually and peaked at S5 (74.84 U g⁻¹ FW). In contrast, the PFK activity in 'Huoju' was the highest in S1 (194.86 U g⁻¹ FW) and then exhibited a sharp and significant decrease by 6.92-fold from S1 to S4 (28.15 U g⁻¹ FW); however, the PFK activity had a slight increment at S5 (28.15 U g⁻¹ FW) (Figure 4c). Overall, the PFK activity in 'Huoju' was obviously and significantly higher than that in 'Qixing' before fruit transitioning (S1–S3), but during the fruit-ripening stages (S4–S6), the PFK activity in 'Qixing' was higher (Figure 4c).

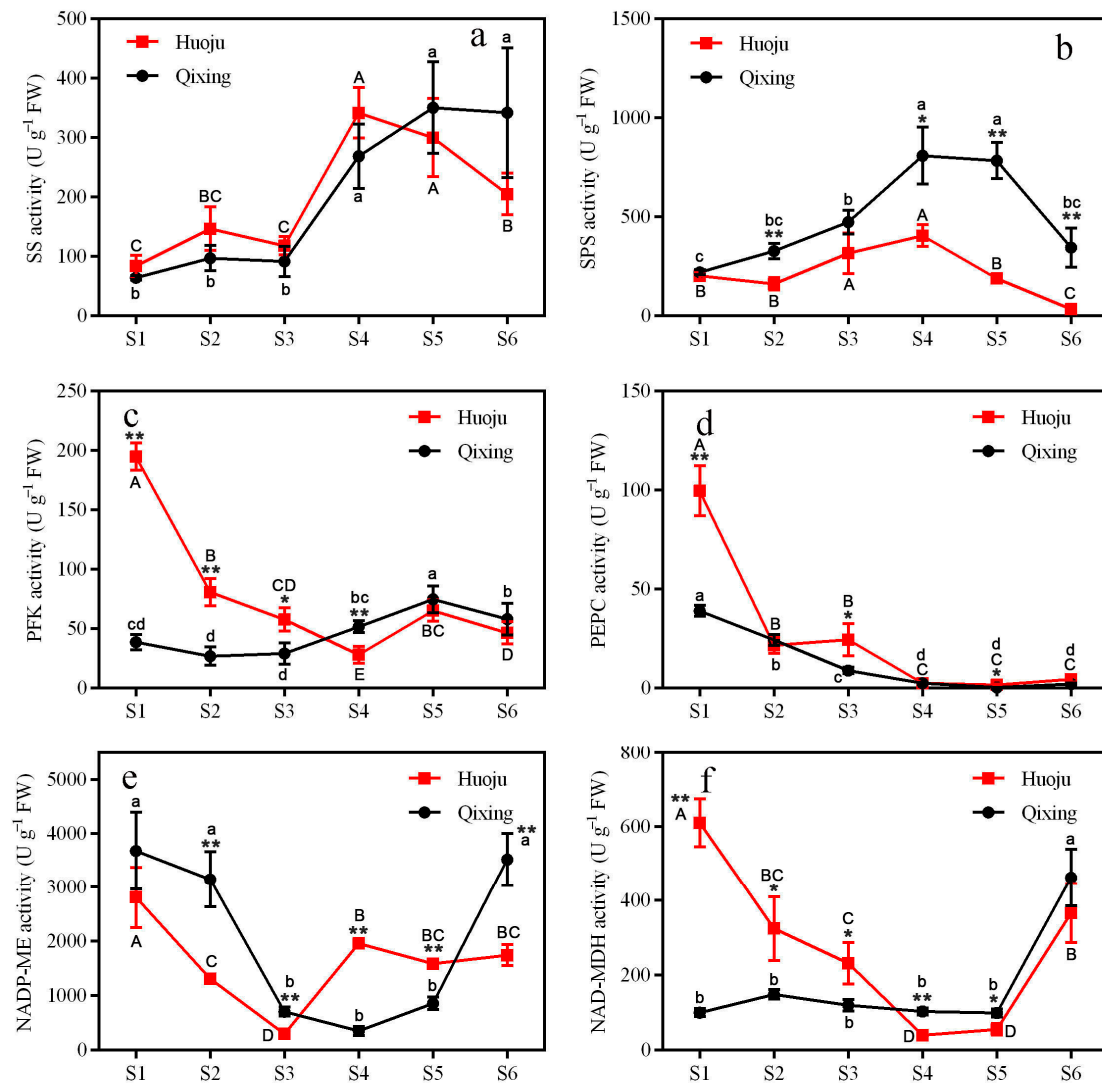


Figure 4. Changes in activities of SS (a), SPS (b), PFK (c), PEPC (d), NADP-ME (e), and NAD-MDH (f) in ‘Qixing’ and ‘Huoju’ fruits at six developmental stages. Bars indicate the standard error (n = 3). One asterisk (*) indicates the significance of each developmental stage between two cultivars based on t-test at $p < 0.05$; two asterisks (**) indicate the significance of each developmental stage between two cultivars based on t-test at $p < 0.01$. Different lowercase letters indicate the significance of six developmental stages of ‘Qixing’ based on Duncan’s test at $p < 0.05$. Different capital letters indicate the significance of six developmental stages of ‘Huoju’ based on Duncan’s test at $p < 0.05$.

The PEPC activity was highest in S1 (39.06 and 99.75 $\text{U g}^{-1} \text{FW}$ in ‘Qixing’ and ‘Huoju’, respectively); then exhibited a marked decline by 14.91- and 39.12-fold from S1 to S4 in ‘Qixing’ and ‘Huoju’, respectively; and remained basically the same during later developmental stages (S4–S6) (Figure 4d). The differences in PEPC activity at S1 and S3 between ‘Qixing’ and ‘Huoju’ were significant (Figure 4d). The activity of NADP-ME decreased continuously and significantly before fruit transitioning (S3) and then increased rapidly and peaked at S6 (3516.55 and 1746.03 $\text{U g}^{-1} \text{FW}$ in ‘Qixing’ and ‘Huoju’, respectively) (Figure 4e). Except for S1, the difference of NADP-ME activities during the other five developmental stages between ‘Qixing’ and ‘Huoju’ were significant (Figure 4e). The NAD-MDH followed a similar pattern to that of NADP-ME. The activity of NAD-MDH before fruit transitioning was obviously higher and significantly in ‘Huoju’ than in ‘Qixing’, but higher during fruit ripening in ‘Qixing’ than in ‘Huoju’ (Figure 4f).

3.4. Correlation Analysis of Sugars, Organic Acids and Metabolic Enzyme Activities During the Development of Loquat

Spearman correlation analysis was performed to evaluate the relationships among sugars, organic acids, and key metabolic enzyme activities across two cultivars and developmental stages (Tables 2 and 3). Based on the correlation strength classification, i.e., $|r| \geq 0.7$ indicated a very strong correlation, $0.5 \leq |r| < 0.7$ indicated a strong correlation, $0.3 \leq |r| < 0.5$ indicated a moderate correlation, and $|r| < 0.3$ indicated a weak correlation, and in the present study, we focused on correlations with $|r| \geq 0.7$ for biological interpretation. The correlations between sugar content, organic acids, and metabolic enzyme activities varied significantly (Tables 2 and 3). In ‘Qixing’, fructose content showed a highly significant positive correlation with that of glucose ($r = 0.935$) and sucrose ($r = 0.966$), but it showed a strong significant negative correlation with sorbitol ($r = -0.871$). Fructose content was also significantly and strongly positively correlated with activities of SS ($r = 0.877$), SPS ($r = 0.591$), and PFK ($r = 0.720$). Fructose was strongly and significantly negatively associated with quinic acid ($r = -0.849$), and acid-related enzyme activity of PEPC ($r = -0.910$) (Table 2). Glucose content was significantly and strongly positively associated with sucrose ($r = 0.867$), and activities of SS ($r = 0.858$), SPS ($r = 0.678$), and NAD-MDH ($r = 0.726$). The level of glucose was significantly and strongly negatively related to sorbitol ($r = -0.687$), quinic acid ($r = -0.705$), and the activity of PEPC ($r = -0.758$) (Table 2). Sucrose content showed a strong significant positive correlation with the activities of SS ($r = 0.891$), SPS ($r = 0.704$), and PFK ($r = 0.804$), but it was significantly and strongly negatively associated with sorbitol ($r = -0.826$), quinic acid ($r = -0.784$), and PEPC activity ($r = -0.870$) (Table 2). Sorbitol content was significantly and strongly positively correlated with quinic acid ($r = 0.954$) and PEPC activity ($r = 0.986$) (Table 2), but it was significantly and strongly negatively related to the activities of SS ($r = -0.682$) and SPS ($r = -0.689$) (Table 2). Malic acid was significantly and strongly negatively related with the activity of PFK ($r = -0.554$) (Table 2). Citric acid was significantly and strongly positively related with the activity of NADP-ME ($r = 0.592$) (Table 2). Quinic acid content was significantly and strongly positively related to the activities of PEPC ($r = 0.976$) and NADP-ME ($r = 0.599$) (Table 2), but it was significantly and strongly negatively related to the activities of SS ($r = -0.681$), and SPS ($r = -0.658$) (Table 2). SS activity was significantly and strongly positively correlated with SPS ($r = 0.551$) and PFK ($r = 0.853$), but it was significantly and strongly negatively correlated with PEPC ($r = -0.753$) (Table 2). SPS activity was significantly and strongly positively related with PFK ($r = 0.506$), but it was significantly and strongly negatively correlated with the activities of PEPC ($r = -0.704$) and NADP-ME ($r = -0.820$) (Table 2). PFK was significantly and strongly negatively correlated with PEPC ($r = -0.573$) (Table 2). PEPC was significantly and strongly positively correlated with NADP-ME ($r = 0.617$) (Table 2).

Table 2. Correlation analysis of sugars, organic acids, and metabolic enzyme activities during fruit development of ‘Qixing’.

	Fructose	Glucose	Sucrose	Sorbitol	Malic	Citric	Quinic	SS	SPS	PFK	PEPC	NADP-ME	NAD-MDH
Fructose	1.000												
Glucose	0.935 **	1.000											
Sucrose	0.966 **	0.867 **	1.000										
Sorbitol	-0.871 **	-0.687 **	-0.826 **	1.000									
Malic	-0.297	-0.354	-0.419	-0.016	1.000								
Citric	-0.164	0.069	-0.237	0.376	0.246	1.000							
Quinic	-0.849 **	-0.705 **	-0.784 **	0.954 **	-0.195	0.150	1.000						
SS	0.877 **	0.858 **	0.891 **	-0.682 **	-0.387	-0.141	-0.681 **	1.000					
SPS	0.591 **	0.324	0.704 **	-0.689 **	-0.069	-0.419	-0.658 **	0.551 *	1.000				
PFK	0.720 **	0.678 **	0.804 **	-0.490 *	-0.554 *	-0.269	-0.438	0.853 **	0.506 *	1.000			

PEPC	−0.910 **	−0.758 **	−0.870 **	0.968 **	−0.036	0.248	0.976 **	−0.753 **	−0.704 **	−0.573 *	1.000		
NADP-ME	−0.378	−0.046	−0.449	0.664 **	−0.203	0.592 **	0.599 **	−0.239	−0.820 **	−0.274	0.617 **	1.000	
NAD-MDH	0.494 *	0.726 **	0.319	−0.255	−0.158	0.369	−0.309	0.394	−0.311	0.140	−0.300	0.494 *	1.000

Notes: One asterisk (*) indicates significance at $p < 0.05$; two asterisks (**) indicate significance at $p < 0.01$.

Table 3. Correlation analysis of sugars, organic acids, and metabolic enzyme activities during fruit development of ‘Huoju’.

	Fructose	Glucose	Sucrose	Sorbitol	Malic	Citric	Quinic	SS	SPS	PFK	PEPC	NADP-ME	NAD-MDH
Fructose	1.000												
Glucose	0.960 **	1.000											
Sucrose	0.930 **	0.832 **	1.000										
Sorbitol	−0.873 **	−0.711 **	−0.896 **	1.000									
Malic	−0.382	−0.537 *	−0.345	−0.026	1.000								
Citric	−0.780 **	−0.632 **	−0.822 **	0.852 **	0.208	1.000							
Quinic	−0.911 **	−0.770 **	−0.914 **	0.992 **	0.051	0.839 **	1.000						
SS	0.676 **	0.598 **	0.827 **	−0.645 **	−0.365	−0.469 *	−0.665 **	1.000					
SPS	−0.176	−0.395	0.138	−0.189	0.386	−0.205	−0.114	0.289	1.000				
PFK	−0.700 **	−0.574 *	−0.731 **	0.843 **	−0.243	0.469 *	0.843 **	−0.639 **	−0.190	1.000			
PEPC	−0.745 **	−0.654 **	−0.727 **	0.805 **	−0.100	0.410	0.830 **	−0.688 **	−0.049	0.951 **	1.000		
NADP-ME	−0.139	0.022	−0.062	0.453	−0.801 **	0.135	0.403	0.059	−0.164	0.578 *	0.527 *	1.000	
NAD-MDH	−0.558 *	−0.377	−0.702 **	0.750 **	−0.112	0.477 *	0.733 **	−0.767 **	−0.460	0.791 **	0.779 **	0.378	1.000

Notes: One asterisk (*) indicates significance at $p < 0.05$; two asterisks (**) indicate significance at $p < 0.01$.

In ‘Huoju’, fructose content was significantly and strongly positively related with glucose ($r = 0.960$), sucrose ($r = 0.930$), and SS activity ($r = 0.676$), but it was significantly and strongly negatively associated with sorbitol ($r = -0.873$); citric acid ($r = -0.780$); quinic acid ($r = -0.911$); and the activities of PFK ($r = -0.700$), PEPC ($r = -0.745$), and NAD-MDH ($r = -0.558$) (Table 3). Glucose content was significantly and strongly positively associated with sucrose ($r = 0.832$) and SS activity ($r = 0.598$), but the level of glucose was significantly and strongly negatively related with sorbitol ($r = -0.711$); malic acid ($r = -0.537$); citric acid ($r = -0.632$); quinic acid ($r = -0.770$); and the activities of PFK ($r = -0.574$) and PEPC ($r = -0.654$) (Table 3). Sucrose content showed a highly significant strong positive correlation with the activity of SS ($r = 0.827$), but it was significantly and strongly negatively associated with sorbitol ($r = -0.896$); citric acid ($r = -0.822$); quinic acid ($r = -0.914$); and the activity of PFK ($r = -0.731$), PEPC ($r = -0.727$), and NAD-MDH ($r = -0.702$) (Table 3). Sorbitol content was significantly and strongly positively related with citric acid ($r = 0.852$); quinic acid ($r = 0.992$); and the activities of PFK ($r = 0.843$), PEPC ($r = 0.805$), and NAD-MDH ($r = 0.750$) (Table 3), but it was significantly and strongly negatively correlated with SS ($r = -0.645$) (Table 3). Malic acid content was significantly strongly negatively correlated with NADP-ME activity ($r = -0.801$) (Table 3). Citric acid content was significantly and strongly positively associated with quinic acid ($r = 0.839$) (Table 3). Quinic acid content was significantly and strongly positively correlated with the activities of PFK ($r = 0.843$), PEPC ($r = 0.830$), and NAD-MDH ($r = 0.733$) (Table 3), but it was significantly and strongly negatively correlated with SS ($r = -0.665$) (Table 3). SS activity was significantly and strongly negatively correlated with the activities of PFK ($r = -0.639$), PEPC ($r = -0.688$), and NAD-MDH ($r = -0.767$) (Table 3). PFK activity was significantly and strongly positively associated with the activities of PEPC ($r = 0.951$), NADP-ME ($r = 0.578$) and NAD-MDH ($r = 0.791$) (Table 3). PEPC activity was significantly and strongly positively related with the activities of NADP-ME ($r = 0.527$) and NAD-MDH ($r = 0.779$) (Table 3).

3.5. Dynamic Changes in Endogenous Phytohormones During Fruit Development in ‘Qixing’ and ‘Huoju’

To clarify the relationship between endogenous phytohormones and loquat fruit flavor formation, the levels of four major phytohormones, IAA, ABA, GA₃, and zeatin, were dynamically analyzed (Figure 5). IAA levels in ‘Qixing’ increased gradually and significantly along with the fruit development and peaked significantly at S4 (315.4 ng g⁻¹ FW), and then they decreased significantly during fruit ripening. In contrast, IAA content in ‘Huoju’ seems to show an opposite trend to that in ‘Qixing’: the IAA content was obviously and significantly high during green-fruit stages (S1–S2), decreased gradually and significantly to the lowest level at S3 (96.3 ng g⁻¹ FW), and then subsequently increased significantly as the fruit ripened (Figure 5a). ABA content during the green-fruit stages (S1–S2) was significantly low in both cultivars. In ‘Qixing’, ABA peaked significantly at S3 (13.4 µg g⁻¹ FW) and then decreased gradually and significantly as fruit ripened. In contrast, ABA in ‘Huoju’ increased sharply, peaked significantly at S5 (37.6 µg g⁻¹ FW), and remained stable at a relatively high level during the mature stages (S4–S6) (Figure 5b). ABA levels during the ripening stages (S1–S2) in ‘Huoju’ were significantly higher than those in ‘Qixing’ at the same period (Figure 5b). GA₃ content in ‘Qixing’ was significantly low during green-fruit stages (S1–S2), increased gradually and significantly after the fruit transitioning stage (S3), peaked significantly at S5 (1126.7 ng g⁻¹ FW), and then decreased significantly as the fruit ripened. Conversely, GA₃ content in ‘Huoju’ exhibited an opposite trend to that in ‘Qixing’: the GA₃ content in ‘Huoju’ was significantly high during the green-fruit stage (S1–S2), with the value of 1700.9 and 1721.4 ng g⁻¹ FW for S1 and S2, respectively; then decreased gradually and significantly to the lowest level at S5 (440.2 ng g⁻¹ FW); and then increased significantly again at S6 (Figure 5c). Zeatin contents in both cultivars showed a similar pattern throughout the developmental stages, increased gradually, and peaked significantly at S5, with the values of 31.9 and 61.3 ng g⁻¹ FW for ‘Qixing’ and ‘Huoju’, respectively (Figure 5d). The differences in zeatin content between ‘Qixing’ and ‘Huoju’ before the fruit transitioning stage (S3) were significant (Figure 5d).

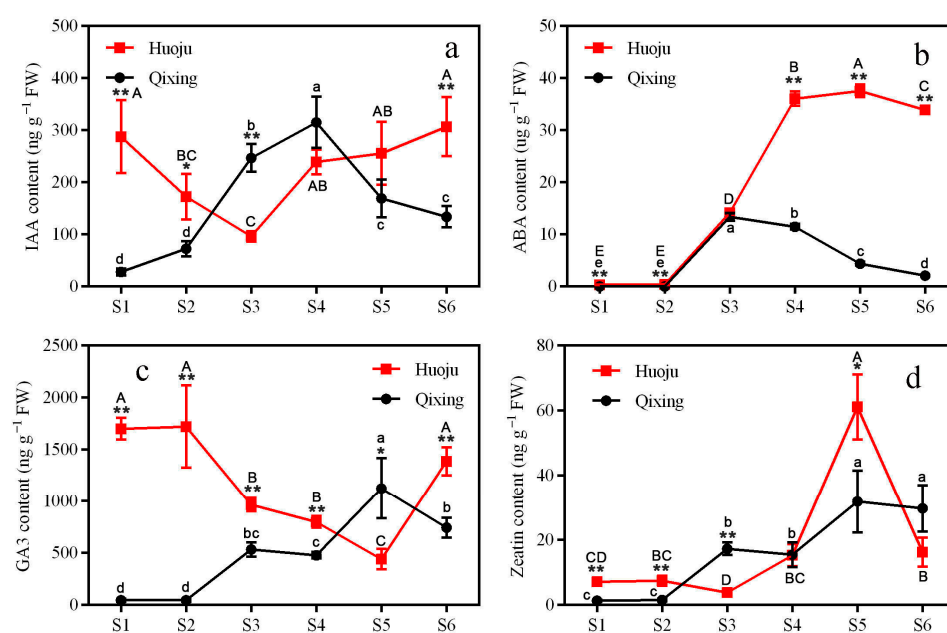


Figure 5. Dynamic changes in endogenous phytohormones indoleacetic acid (a), abscisic acid (b), gibberellin (c), and zeatin (d) in developmental fruits of ‘Qixing’ and ‘Huoju’. The bar indicates the standard error (n = 3). One asterisk (*) indicates the significance of each developmental stage

between two cultivars based on t-test at $p < 0.05$; two asterisks (**) indicate the significance of each developmental stage between two cultivars based on t-test at $p < 0.01$. Different lowercase letters indicate the significance of six developmental stages of 'Qixing' based on Duncan's test at $p < 0.05$. Different capital letters indicate the significance of six developmental stages of 'Huoju' based on Duncan's test at $p < 0.05$.

4. Discussion

Sugar and organic acids are the major soluble components of fruits and play crucial roles in determining fruit quality and flavor [34]. Fructose, sucrose, glucose, and sorbitol are the main sugars in fruits that gradually accumulate during maturation [18,35]. In the present study, fructose and sucrose were identified as the dominant sugars in loquat (Figure 2), consistent with the findings of Yang et al. (2021) [10]; however, this was slightly different from the report published by Xu and Chen (2011) [8], in which glucose and fructose were considered the dominant sugars and accounted for at least 80% of the total sugar in loquat fruit. This inconsistency in the abundance of sugars might have resulted from differences in the tested varieties and corresponding cultivation conditions. In this work, the contents of fructose and glucose in both 'Qixing' and 'Huoju' were significantly low during early green-fruit stages (S1–S2), but they increased sharply and significantly along with fruit development (Figure 2a,b). Similar dynamic changes in fructose and glucose content were reported by Yang et al. (2021) [10] and Qin et al. (2012) [14]. The increase in fructose and glucose levels results from the combined action of multiple enzymes. Our data showed a significant strong positive correlation between SS and PFK activity, and fructose and glucose content in white-fleshed cv. 'Qixing' (Table 2), whereas in red-fleshed cv. 'Huoju', fructose and glucose contents were significantly strongly positively associated with SS activity but strongly negatively correlated with PFK activity (Table 3), indicating that fructose and glucose content and enzyme activity might differ owing to the flavor and flesh type of loquat fruit. In addition to fructose and glucose, sucrose content was also significantly high in loquats during the mature stages (S4–S6) of development (Figure 2a–c). Specifically, the fructose and sucrose contents, especially the sucrose content, in white-fleshed high-sugar 'Qixing' were significantly higher than those in red-fleshed sour-sweet 'Huoju' during ripening stages of S4–S6 (Figure 2a,c), while the glucose in 'Huoju' was always significantly higher than that in 'Qixing' (Figure 2b). This was consistent with the point that fructose and sucrose contribute more to sweet taste of loquats fruits than glucose [10,36]. Additionally, the negative correlation between SS activity and sorbitol content ($r = -0.682$ and -0.645 for 'Qixing' and 'Huoju', respectively) deserves particular attention. Unlike SPS, which primarily catalyzes sucrose synthesis, SS predominantly functions in the sucrose cleavage direction in fruits, generating fructose and UDP-glucose for metabolic utilization. The negative correlation observed in present might suggest that when SS activity was elevated, more sucrose was cleaved rather than accumulated, potentially reducing the substrate available for sorbitol synthesis, which provides new insights into the competitive partitioning of carbon between sucrose and sugar alcohols in loquat. Interestingly, during the entire fruit development process, sucrose did not continue to increase like fructose and glucose; instead, it decreased slightly but significantly in the late stages (S5–S6) of fruit development (Figure 2c), which might be explained by sucrose being degraded into hexose in the late developmental stages [37]. SS and SPS play vital roles in sucrose accumulation [38,39]. This study showed a strong positive correlation between sucrose content and SS activity in both cultivars (Tables 2 and 3). Sugar accumulation is a complex physiological process that involves the synthesis, transport, unloading, transformation, and storage of photosynthetic assimilates. In addition, changes in sugar content are also closely related to the cultivated variety and cultivation methods, such as bagging [40] and fruit thinning [41].

Organic acids are another component that plays an important role in regulating loquat fruit flavor, and the balance between organic acids and sugars largely determines the fruit texture and, thus, consumer preferences [42]. Generally, the organic acid content in red-fleshed loquats, classified as the high-acid category, is relatively higher than that in white-fleshed loquats, clustering into low-acid groups; therefore, the taste of red-fleshed varieties is usually more acidic than that of white-fleshed varieties [19]. In this present work, 'Huoju' was a red-fleshed variety with sweet and sour flavor, while 'Qixing' was a white-fleshed variety with sweet taste; however, the TA of 'Qixing' in the whole developmental stages was interestingly higher than that of 'Huoju' (Figure 3a). Therefore, three organic acids were further evaluated in the loquat fruit: quinic, citric, and malic acids (Figure 3b–d), as well as the acid-associated enzymes PEPC, NAD-MDH, and NADP-ME (Figure 4d–f). The results showed that malic acid was the predominant organic acid detected in loquat fruits. The dynamic changes in malic acid in both cultivars were almost the same (Figure 3c), whereas citric and quinic acids content were significantly high before fruit color changed (S3) and decreased significantly to extremely low levels during the fruit-ripening stages (S4–S6) (Figure 3b,d). The coloration period is a pivotal phase in the transition of fruits from the growth to the maturation phase. The rapid decline in organic acids, accompanied by sugar accumulation (Figure 2a–c), has been shown to significantly increase the sugar–acid ratio of the fruit and improve its palatability. Based on these, the difference in taste of 'Qixing' than 'Huoju' might result from the higher sugar level (i.e., fructose and sucrose) during the ripening stage in 'Qixing' fruits (Figure 2a,c). This is consistent with the conclusion that the better taste of white-fleshed loquat might be mostly due to its high fructose and low malic acid contents [42]. Changes in organic acids during fruit development are usually the result of their synthesis, degradation, and redistribution [43]. PEPC is a pivotal rate-limiting enzyme in organic acid synthesis, and the levels of quinic and citric acids are closely associated with PEPC activity [44,45]. In this study, the dynamic changes in PEPC enzyme activity (Figure 4d) almost synchronously corresponded to the curves of quinic acid and citric acid content (Figure 3b,d). Moreover, the correlation analysis indicated a strong positive relationship between PEPC activity and quinic acid content, both in 'Qixing' and 'Huoju' (Tables 2 and 3), a finding that further agrees with the statement mentioned above. NAD-MDH is predominantly implicated in the redox balance of malic acid, and differences in malic acid concentration among different loquat varieties may be attributed to differences in NAD-MDH activity among cultivars [24]. A linear correlation between malic acid level and NAD-MDH activity was found in high-acid 'Jiefangzhong' and low-acid 'Changhong 3' [24]. In the present work, the levels of malic acid in 'Qixing' and 'Huoju' both showed a trend of first increasing and then decreasing (Figure 3c); however, the changes in NAD-MDH activity were obviously different between 'Qixing' and 'Huoju' (Figure 4f). Moreover, a negative correlation between malic acid level and NAD-MDH activity was suggested both in 'Qixing' and 'Huoju' (Tables 2 and 3), which differed from the conclusion proposed by Chen et al. (2009) [24]. This inconsistency could be explained by the differences among loquat varieties, or the different flesh types of loquats. NADP-ME is involved in the degradation of organic acids via decarboxylation [46]. In the present work, the activities of NADP-ME in 'Qixing' and 'Huoju' both showed an "up–down–up" trend (Figure 4e), and a strong negative correlation between malic acid level and NADP-ME activity was found in 'Huoju' (Tables 2 and 3).

Plant hormones such as auxin, gibberellin, abscisic acid, and zeatin also play important roles in regulating fruit quality, and the balance and interactions among endogenous phytohormones are particularly critical for loquat quality formation [47–49]. In the early stages of fruit development, auxin and IAA have been suggested as important factors determining the size and shape of the fruit [50–52]. During the late stages of fruit development, auxin regulates the transport and distribution of assimilates to the fruit,

thereby indirectly affecting sugar accumulation [53,54]. Interestingly, in this work, the sugar-content changes in ‘Huoju’ and ‘Qixing’ were generally similar (Figure 2), but the auxin level in both cultivars showed opposite trends (Figure 5a). This might be explained by the fact that ‘Huoju’ had a larger fruit size than ‘Qixing’, while the total sugar content in ‘Qixing’ was obviously higher than in ‘Huoju’. GA works synergistically with auxin to promote fruit enlargement; however, its role in the maturation period is usually related to delayed senescence and the inhibition of coloration [55,56]. In this study, the change in GA3 levels was basically the same as that of auxin (Figure 5a,c), consistent with the description above. ABA has traditionally been regarded as a dormancy-inducing and abscission-promoting hormone; however, in the regulation of fruit quality, its role in promoting ripening is more prominent [57,58]. During the later stages of fruit development, the ABA content rises sharply, becoming a key signal for initiating fruit ripening [59]. At the same time, ABA may regulate organic acid metabolism, thereby ultimately determining the unique sugar–acid ratio and flavor of loquat fruits [60]. In this study, ABA content in ‘Huoju’ was relatively low during the early fruit development stage, and then it increased along with fruit development and peaked during the ripening stage (Figure 5b), while in ‘Qixing’, the ABA in the late development stage decreased to a relatively low level (Figure 5b). This might be due to ‘Qixing’ being a white-fleshed type, and ‘Huoju’ being a red-fleshed type. CTKs have also been suggested to play important roles in fruit development, and CTKs and auxins work together to regulate fruit enlargement [61,62]. However, in this study, the dynamic changes in zeatin seemed not to be in sync with those of auxin, especially in ‘Huoju’ (Figure 5a,d). Overall, the development and flavor formation of loquats are complex physiological and ecological processes, and the levels of sugar, organic matter, enzyme activities, and plant hormones might be influenced by multiple factors, including the tested varieties, fruit flesh types, sampling periods, and fruit-maturity consistency.

5. Conclusions

In summary, this study systematically investigated the dynamic changes in sugars, organic acids, and phytohormones, and the activities of key sugar- and acid-metabolism-related enzymes during fruit development in the white-fleshed, high-sugar cultivar ‘Qixing’ and the red-fleshed, sour–sweet cultivar ‘Huoju’. The findings demonstrate that the sugar-accumulation enzymatic module (PFK, SPS, and SS) is positively correlated with soluble sugar content, whereas the organic acid metabolic module (PEPC, NADP-ME, and NAD-MDH) precisely modulates acid degradation rates; the synergistic action of these two modules determines the cultivar-specific flavor. At the hormonal level, IAA and GA₃ play vital roles in fruit enlargement, while ABA is important for fruit ripening, triggering sugar accumulation and organic acid reduction. Collectively, these findings advance the understanding of the physiological basis of loquat quality formation, providing a theoretical foundation for breeding high-sugar, high-quality loquat cultivars.

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