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Inheritance of Fruit Weight, Size and Organic Acid Content in a Distant Hybrid Population of Longan 'Huanongzao' and Lychee 'Ziniangxi'

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Abstract: The type and content of organic acids in fruits are important factors that determine the traits, such as the nutrition and flavor of fruits. Fruit weight and size are also very important economic characters in fruit breeding research. To investigate the inheritance patterns in longan, fruit organic acid contents, weight, and size were measured in the distant hybridization progenies of longan 'Huanongzao' and lychee 'Ziniangxi'. The results revealed that the malic acid accumulation exhibited mid-parent heterosis, citric acid content showed a tendency towards depression, and oxalic acid, ketoglutaric acid, fumaric acid, gallic acid, and total acid contents exhibited transgressive inheritance. The inheritance patterns in fruit weight, length and diameter tended towards smaller and degraded. The coefficient of variation (CV) for the organic acids ranged from 35.77–90.20%, and the heritability (H^2) was 72.35–97.44%. High CV (55.44%) coupled with medium H^2 (28.72%) were observed in fruit weight, however, low CV (12.29% and 12.50%) coupled with high H^2 (68.95% and 69.25%) were shown in fruit length and diameter. In this study, the genetic variation of acid contents, fruit weight and size in the F_1 population of longan and lychee were analyzed for the first time, providing an informative and theoretical basis for the selection and breeding of longan cultivars.

Keywords: longan; intergeneric hybridization; high-performance liquid chromatography; fruit quality; genetic analysis

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1. Introduction

Longan (*Dimocarpus longan* Lour.) is a plant that belongs to the genus *Dimocarpus* in the family Sapindaceae [1]. China is the center of origin of longan and ranks first in longan plantation area and production worldwide. However, the irrational composition of cultivars, lack of high-quality cultivars, and dominant production regions of longan have led to a decline in the competitiveness of China's longan in the international market in recent years. This has seriously impacted the development of China's longan industry. Germplasm innovation is the key to solving this problem, but artificial selection has resulted in a narrow genetic background in longan varieties, as it is a woody perennial. This problem has not been solved, despite the effort put into selective breeding of 37 new cultivars in China, through seedling selection and hybridization, since the late 1980s [2]. Therefore, it is crucial to discover and utilize the advantageous genetic resources between various genera, to develop new breeding methodologies. In this regard, distant hybridization seems to be an important method by which to achieve gene transfer between genera [3].

As important constituents of a fruit's flavor and nutrients, organic acids affect their taste, color and biostability, and provide important information on their ripeness, storability, and processability [4]. Fruit weight and size are important business and breeding indicators

as they are the priority morphological characteristics to be observed by consumers [5]. Thus, exploring the inheritance patterns of organic acid, weight and size traits in fruits is of great importance in the research on fruit-tree breeding. Studies on this issue have been conducted in fruits such as apple [6], pear [7], grape [8], mango [9], blueberry [10], jujube [11], plum [5] and coconut [12]. However, very few studies have focused on longan, they have only analyzed the organic acid content in fruits of different varieties [13,14]. Therefore, it is necessary to conduct inheritance studies on the organic acid content, fruit weight and size in longan.

To resolve the lack of large-fruited high-quality longan cultivars in China, this study extended the traditional hybridization mode of longan breeding through distant hybridization of longan 'Huanongzao' with lychee 'Ziniangxi'. The characteristics of the organic acid components, fruit weight and size, and their inheritance patterns were analyzed in the F_1 hybrids. We report for the first time the inheritance trend of different organic acid constituents, fruit weight, length and diameter in the longan-lychee distant hybrid progenies, thereby providing novel ideas for the selection of longan hybrid parents and a theoretical basis for the selection and breeding of longan cultivars.

2. Materials and Methods

2.1. Plant Material and Main Reagents

A longan distant hybrid population derived from a cross of 'Huanongzao' and 'Ziniangxi' was generated in 2012. A total of 187 individuals were produced, of which 101 individuals bearing fruits, and their parents, were used for fruit quality analysis. The female parent of 'Huanongzao' was an early-maturing longan cultivar, and the male parent of 'Ziniangxi' was a high-quality lychee cultivar with large fruit (Figure 1). The F_1 hybrids were planted at the National Tropical Fruit Tree Germplasm Resource Park, South Subtropical Crops Research Institute, Chinese Academy of Tropical Agricultural Sciences (CATAS), 21°10′2″ N, 110°16′34″ E. Mature and healthy fruits were harvested in May ('Ziniangxi') and from late June to early July ('Huanongzao' and 101 F_1 hybrids) between 2020 and 2021. Samples were stored at 4 °C for fruit weight and size measurement, and peeled, pitted, snap-frozen in liquid nitrogen, and stored at −80 °C until organic acid content determination.

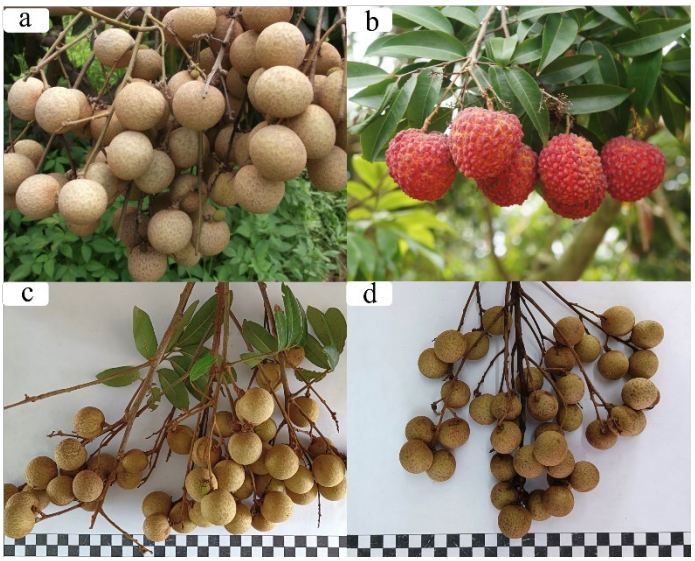

Figure 1. The mature fruit of 'Huanongzao', 'Ziniangxi' and two F_1 hybrids. Note: (**a**): 'Huanongzao'; (**b**): 'Ziniangxi'; (**c**): F_1 hybrid 'HZ3'; (**d**): F_1 hybrid 'HZ9'.

The HPLC-grade organic acid standards (oxalic acid, malic acid, ketoglutaric acid, citric acid, fumaric acid, and gallic acid) and metaphosphoric acid were purchased from Shanghai Yuanye Biotechnology Co., Ltd. (Shanghai, China). HPLC-grade methanol was procured from Sigma (St. Louis, MO, USA).

2.2. Extraction of Organic Acids from the Hybrid Population Fruit

The organic acids were extracted using the method described by Zhang et al. [15], with slight optimization. Briefly, longan fruit pulp was crushed and mixed well, through freezing with liquid nitrogen. A total of 1.0 g of the crushed pulp was weighed accurately, and 5 mL of metaphosphoric acid (2 g/L) was added to it. The mixture was further ground in an ice bath and centrifuged at 10,000 rpm for 15 min, to separate and collect the supernatant; the pellet was mixed with 4 mL of metaphosphoric acid for a thorough wash, and centrifuged to collect the supernatant. The supernatants from both steps were combined, and the final volume was adjusted to 10 mL with metaphosphoric acid. After rigorous shaking and mixing, 1 mL of each sample was filtered through a 0.45 μm filter for the following tests. Each sample was repeated three times.

2.3. Determination of Organic Acid Content in the Hybrid Population Fruit

The organic acid content in the parent and hybrid fruits was determined using HPLC. Agilent 1260 ultra-high performance liquid chromatography system, with a VWD UV detector and a C18 column (250 mm × 4.6 mm, 5 μm), were used. The mobile phase was prepared using 90% metaphosphoric acid (2 g/L) and 10% methanol, and the flow rate was set to 1 mL/min. The column temperature was set to 35 °C, and the injection volume was 10 μL, with a detection time of 10 min per sample.

About 1 mL of each prepared sample was aspirated, filtered through a 0.45 μm filter, and analyzed using the above-mentioned HPLC system. Each sample was repeated three times. Relative standard curves were used for comparison, to accurately determine the concentrations of organic acids in mg/g fresh weight (FW).

2.4. Calculation of Organic Acid Content in the Hybrid Population Fruit

The content of each organic acid constituent in the hybrid population fruits was calculated using the equation

$$X = C \times V/M,$$

where: X is the content of the organic acid (mg/g FW) in each longan hybrid progeny; C is the calculated concentration of each organic acid (mg/mL), using the linear regression equation; V is the fixed volume (mL) of the sample; and M is the mass of the pulp to be measured (g). Total acid = oxalic acid + malic acid + ketoglutaric acid + citric acid + fumaric acid + gallic acid.

2.5. Measurement of Fruit Weight and Size in the Hybrid Population

Each F_1 hybrid owns 1 to 4 fruit clusters, each with about 30 to 150 fruits. A total of 20 healthy fruits were randomly selected from each individual, to measure single fruit weights with an electronic scale, and fruit length and diameter, with a digital vernier caliper, along the center direction of each fruit. Each indicator was repeated ten times.

2.6. Genetic Analysis of Organic Acids in the Hybrid Population Fruit

Statistical analysis of the hybrid progeny mean (F), mid-parent value (MP), coefficient of variation (CV), broad-sense heritability (H^2) and transgressive inheritance rate for each organic acid component, and fruit quality, of longan hybrid was performed using Excel 2010 and software SPASS 19, calculated as specified by Liu et al. [16] and Qian et al. [17]:

$$CV = \sigma/F \times 100\%;$$

$$H^2 = [V_H - 1/2(V_{p1} + V_{p2})]/V_H \times 100\%.$$

where: σ represents the standard deviation; V_H is the phenotypic variance of the hybrid population; V_{p1} is the female parent phenotypic variance; V_{p2} is the male parent phenotypic variance.

CV reflects the relative dispersion between variables. And H^2 refers to the proportion of genetic variance to the total observed variance in the population.

3. Results

3.1. Organic Acid Components and Linear Regressions

The composition of the organic acid standards was examined and oxalic acid, malic acid, ketoglutaric acid, citric acid, fumaric acid, and gallic acid were detected at 2.436, 2.851, 3.290, 3.796, 4.834, and 6.053 min, respectively (Table 1).

Table 1. The peak time, linear relationship and correlation coefficient for each acid component.

Organic Acid Species	Peak Time (min)	Linear Relationship Equation	Correlation Coefficient
Oxalic acid	2.436	y = 0.1518x − 1.1774	R^2 = 1.0000
Malic acid	2.851	y = 0.2989x − 0.6368	R^2 = 1.0000
Ketoglutaric acid	3.290	y = 0.2353x − 0.5160	R^2 = 1.0000
Citric acid	3.796	y = 1.7660x − 0.9855	R^2 = 1.0000
Fumaric acid	4.834	y = 0.0128x − 0.2030	R^2 = 0.9994
Gallic acid	6.053	y = 0.0140x + 0.1313	R^2 = 0.9999

A series of dilutions of the standards of mixed organic acids were examined. The peak area was indicated on the *X*-axis and the concentration of organic acid (mg/g FW) on the *Y*-axis, to plot the standard curve for each acid, and the correlation equation and correlation coefficient for each acid were calculated accordingly.

3.2. Analysis of Organic Acid Content in F_1 Hybrids

The results of this study revealed that the organic acid content in the hybrid of 'Huanongzao' × 'Ziniangxi' progeny was widely segregated (Table 2). The content of oxalic acid, malic acid, ketoglutaric acid, citric acid, fumaric acid, and gallic acid exhibited significant variation, ranging between 0.397–4.479, 1.454–6.330, 0.015–0.736, 0.154–1.804, 0.012–0.129, and 0–0.0013 mg/g FW, respectively. The main organic acids accumulated in the fruit of 'Huanongzao' were malic acid and oxalic acid, while those in the fruit of 'Ziniangxi' were malic acid and citric acid. Gallic acid was not detected in the fruit of 'Ziniangxi' and 13 hybrids. All the organic acid in the longan hybrid progeny conformed to the normal distribution with continuous variability, thereby indicating that the acid content is a quantitative trait, controlled by polygenes.

Table 2. Estimates of variability and genetic parameters for organic acid content in 101 hybrids and their parents.

Organic Acid Species	Female (mg/g FW)	Male (mg/g FW)	MP (mg/g FW)	Range (mg/g FW)		F (mg/g FW)	CV (%)	H^2 (%)	LL (%)	HH (%)
				Min	Max					
oxalic acid	1.725 ± 0.025	0.371 ± 0.070	1.048	0.397 ± 0.042	4.479 ± 0.305	1.687	45.88	97.44	0	42.45
Malic acid	3.509 ± 0.214	2.154 ± 0.700	2.831	1.454 ± 0.123	6.330 ± 0.123	2.824	35.77	93.86	21.70	17.92
Ketoglutaric acid	0.101 ± 0.004	0.046 ± 0.004	0.074	0.015 ± 0.001	0.736 ± 0.014	0.204	90.20	72.35	8.49	71.70
Citric acid	1.338 ± 0.041	0.632 ± 0.119	0.985	0.154 ± 0.001	1.804 ± 0.078	0.740	50.19	82.30	33.02	2.83
Fumaric acid	0.042 ± 0	0.017 ± 0.005	0.029	0.012 ± 0	0.129 ± 0.027	0.040	75.24	46.15	8.49	33.02
Gallic acid	0.004 ± 0	0 ± 0	0.002	0 ± 0	0.013 ± 0.001	0.006	55.57	96.15	0	74.53
Total acid	6.719 ± 0.278	3.220 ± 0.678	4.969	3.013 ± 0.094	10.162 ± 0.192	5.501	29.28	94.11	2.83	20.75

Note: Female: 'Huanongzao'; Male: 'Ziniangxi'; MP: mid-parent value; F: hybrid progeny mean; CV: coefficient of variation; H^2: heritability; LL: the ratio of lower than low parent; HH: the ratio of higher than high parent. CV: low = 0–10%; medium = 10–20%; high = 20% and above; H^2: low = less than 30%; medium = 30–60%; high = more than 60%.

3.3. Inheritance Analysis of Organic Acid Content in Longan Hybrid Progeny

As shown in Table 2, the mean value of the malic acid content in the hybrid progeny (2.824 mg/g FW) was close to the mid-parent value (2.831 mg/g FW), thereby indicating both 'Huanongzao' and 'Ziniangxi' affected malic acid in progenies. The mean value of the citric acid content in the hybrid progeny (0.740 mg/g FW) was lower than the mid-parent value (0.985 mg/g FW) and was closer to that in male 'Ziniangxi' (0.632 mg/g FW), showing a tendency of depression, which was mainly influenced by the additive genetic effects. The ratio of lower than low parent (LL, 21.70%; 33.02%) was higher than the ratio of higher than high parent (HH, 17.92%; 2.83%) for both malic and citric acid contents in the hybrids, and more progeny plants tended towards the paternal parent.

Moreover, the mean values of oxalic acid, ketoglutaric acid, fumaric acid, gallic acid and total acid contents of the hybrid progeny (1.687 mg/g FW; 0.204 mg/g FW; 0.040 mg/g FW; 0.006 mg/g FW; and 5.501 mg/g FW, respectively) were all higher than the mid-parent values (1.048 mg/g FW; 0.074 mg/g FW; 0.029 mg/g FW; 0.002 mg/g FW and 4.969 mg/g FW, respectively), and closer to the maternal parent, 'Huanongzao'. These results imply that oxalic acid, ketoglutaric acid, fumaric acid, gallic acid and total acid contents exhibit transgressive inheritance and are influenced by both additive and non-additive genetic effects. Their HH reached 17.92%, 71.70%, 33.02%, 74.53% and 20.75%, respectively, exhibiting high transgressive inheritance. These results indicate a higher probability of selecting longan cultivars with high acid content from this cross combination.

The coefficient of variation for six organic acids ranged from 35.77–90.20%, thereby indicating the selection potential of organic acids is great. The heritability of almost all organic acids ranged from 72.35–97.44%, indicating their variation mainly resulted from inheritance, except fumaric acid (46.15%), with the variation being caused by both environmental factors and inheritance.

3.4. Inheritance Analysis of Fruit Weight and Size of Longan Hybrid Progeny

F_1 hybrids are similar to the female parent 'Huanongzao' in their morphological manifestation (Figure 1). As shown in Table 3, the fruit weight of the female parent 'Huanongzao' was 9.23 g, the male parent 'Ziniangxi' was 55.28 g and F_1 hybrids ranged from 5.83 to 14.18 g. The maximum fruit weight among 101 hybrids (14.18 g) was 1.54 times that of 'Huanongzao'. Moreover, there were 26 F_1 hybrids whose fruit weighed more than 10.00 g, representing 25.74% of all hybrids. The fruit weight mean value of the hybrid progeny (9.26 g) was far lower than the mid-parent value (32.25 g), but close to the female parent value (9.23 g), thereby indicating that 'Huanongzao' mainly affected fruit weight in progenies. The CV was classified as high (55.44%); however, heritability was medium (28.72%).

Table 3. Estimates of variability and genetic parameters for fruit characteristics in 101 hybrids and their parents.

Fruit Character	Female	Male	MP	Range		F	CV (%)	H^2 (%)	LL (%)	HH (%)
				Min	Max					
Fruit weight (g)	9.23 ± 0.80	55.28 ± 1.87	32.25	5.83 ± 0.68	14.18 ± 1.28	9.26	55.44	28.72	45.45	0.00
Fruit length (mm)	24.72 ± 1.94	45.34 ± 1.91	35.03	11.92 ± 0.91	28.01 ± 1.17	24.15	12.29	68.95	61.36	0.00
Fruit diameter (mm)	26.15 ± 2.44	49.59 ± 1.82	37.87	14.22 ± 0.79	31.11 ± 1.41	26.22	12.50	69.25	44.32	0.00

Note: Female: 'Huanongzao'; Male: 'Ziniangxi'; MP: mid-parent value; F: hybrid progeny mean; CV: coefficient of variation; H^2: heritability; LL: the ratio of lower than low parent; HH: the ratio of higher than high parent. CV: low = 0–10%; medium = 10–20%; high = 20% above; H^2: low = less than 30%; medium = 30–60%; high = more than 60%.

The fruit length and diameter of F_1 hybrids ranged between 11.92–28.01 mm and 14.22–31.11 mm, respectively. The mean values of fruit length and diameter of the hybrid progeny (24.15 and 26.22 mm) were all close to female parent values (24.72 and 26.15 mm). The CV was classified as low (12.29% and 12.50%); however, H^2 was high (68.95% and 69.25%).

The LLs of fruit weight, length and diameter were up to 45.45%, 61.36%, and 44.32%, respectively, indicating that the fruit weight of hybrid progenies tended to become smaller.

4. Discussion

The study on the organic acid constituents of longan fruit found that the proportion of organic acids in the fruit varied in different varieties of longan, with malic acid representing the highest acid content followed by oxaloacetic acid and ketoglutaric acid [13]. Moreover, the major organic acids in 'Shixia' and 'Chuliang' were malic acid, tartaric acid, and citric acid, while fumaric acid was undetected [18]. However, the organic acids in 'Huanongzao' and 101 F_1 hybrids in this study were mainly malic acid, oxalic acid, and citric acid, but fumaric acid was also detected. The research has shown that the acids in lychee were mainly malic acid, succinic acid, and citric acid [19], although Hu et al. [20] suggested malic acid and tartaric acid. In this study, the organic acids in 'Ziniangxi' were mainly malic acid and citric acid; gallic acid was undetected. Gallic acid was also not detected in the fruits of the 13 hybrids, which could make the flavor of these fruits an interesting topic for further investigation.

The malic acid content was reported as transgressive inheritance in grape [21] and apricot [22]. However, the malic acid content of the F_1 generation of 'Huanongzao' × 'Ziniangxi' was close to the mid-parent value. The result was consistent with berries by Guo et al. [8]. The trait inheritance of citric acid content in apricot was found to be influenced by a combination of additive and non-additive effects [23]. However, the results of our study are concordant with the findings of Jiang et al. [22], which suggested that the citric acid trait inheritance was mainly affected by the additive effects and showed a tendency of depression. Conversely, oxalic acid, ketoglutaric acid, fumaric acid, and gallic acid exhibited transgressive inheritance under the co-influence of additive and non-additive effects. In contrast to the conclusion in apple—where oxalic acid content is a discontinuously variable quality trait controlled by multiple genes and influenced by micro-effective polygenes [24]—the results of this study revealed that the oxalic acid content varied continuously with the normal distribution, and was a quantitative trait controlled by multiple genes. The mean value of the total acid content was higher than the mid-parent value, indicating transgressive inheritance. This conclusion is in agreement with the findings in grape [8], pear [7], and blackcurrant [25].

A high HH was found in the progeny of 'Huanongzao' × 'Ziniangxi'. This is probably because the organic acid content is a quantitative trait controlled by multiple genes, which exerts not only additive, but also non-additive effects, to a certain extent. When these genes undergo recombination during sexual hybridization, they exert new non-additive effects with the generation of transgressive individuals. The range of CV above 20% was classified as high, as suggested by Sivasubramanian and Madhavamenon [26]. The CV of the total acid content in the hybrid progeny fruit was 29.28%, indicating a high genetic potential and a wide variety for selection. The H^2 of the total acid reached up to 94.11%, showing the population has high heritability in organic acid content, and can generate relatively stable inheritance.

In the fruit weight and size study, there was no transgressive inheritance shown in distant hybrid progenies of either longan or lychee. Fruit weight, length and diameter mean values of the hybrids were far lower than the mid-parent values, indicating that inheritance trends of fruit weight and size tended towards smaller and degraded. The results were in accordance with previous research in longan [27,28], implying that there was a negative non-additive effect on the inheritance of fruit weight in longan. Similar results have been confirmed in other fruit trees, such as, jujube [11], plum [12] and grape [29]. Despite the LL of fruit weight being very high, there were 25.74% of offspring whose fruit weight more than 10 g. These offspring would provide valuable germplasm resources for longan big-fruit breeding. Corresponding with the research in jujube [11], the CV of longan fruit weight (55.44%) was significantly greater than that of fruit length and diameter (12.29% and 12.50%). Therefore, the selection potential of fruit weight was higher than that of fruit length and diameter. However, compared to fruit weight, there was higher heritability in

both fruit length and diameter (28.72% vs. 68.95% and 69.25%, respectively). Fruit weight was more susceptible to environmental factors.

5. Conclusions

In summary, we report the first organic acid, fruit weight and size inheritance patterns conducted in distant hybrid populations of longan and lychee. In this study, the content values of six organic acids in 101 individuals were determined by using HPLC. Among them, malic acid, oxalic acid and citric acid were the main organic acids in the F_1 progeny. High-acid varieties are more likely to be selected from the cross combinations, due to the prevalence of transgressive inheritance in the F_1 hybrids. The inheritance patterns in fruit weight and size tended, predominantly, towards smaller, although 25.74% of the hybrids fruit weight reached more than 10.00 g. The total acid content had a high CV (29.28%) and heritability (94.11%). Fruit weight had a high CV (55.44%) and medium H^2 (28.72%); however, fruit length and diameter had a low CV (12.29% and 12.50%) and high H^2 (68.95% and 69.25%). These results will provide an important theoretical basis for the selection and breeding of longan cultivars.

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