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Research Article

Comparative biochemical analysis and profiling of sucrose-metabolizing enzyme activity in female and hermaphrodite papaya fruits at different phenological stages

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Abstract

Papaya (*Carica papaya* L.) is widely recognized as a nutraceutical or functional fruit due to its rich nutritional and medicinal properties. This study presents a comparative analysis of female and hermaphrodite papaya fruits at three phenological stages (mature, intermediate, and green), evaluating physical parameters (fruit and seed), biochemical composition (carbohydrates, proteins, and reducing sugars), and organoleptic properties of fruits. Enzymatic activities of sucrose synthase (SuSy), sucrose phosphate synthase (SPS), and acid invertase (AI) were assessed across maturity stages in both fruit types. Organoleptic evaluation revealed distinct preferences, with mature fruits of both types receiving favorable scores. Notably, female papayas were rated higher in aroma, flavor, and overall acceptability. Biochemical analysis indicated that female fruits contained higher levels of protein, reducing sugars, and carbohydrates. Enzymatic activity varied significantly with maturity: AI activity peaked in mature fruits but was lower in younger stages, whereas SuSy activity was highest in green fruits and declined with ripening. SPS activity remained stable in both fruit types. These findings suggest that AI and SuSy play pivotal roles in sugar accumulation during ripening, influencing fruit sink strength during development. This study compares sugar metabolism and consumer preference in female and hermaphrodite papayas to determine which yields sweeter fruit. The findings will guide improved cultivation practices and advance understanding of papaya fruit quality.

Keywords: Acid invertase; Hermaphrodite papaya fruits; Papaya sweetness; Sucrose phosphate synthase; Sucrose synthase; Sugar metabolizing enzyme

Introduction

Papaya (*Carica papaya* L.) is a tropical fruit with a distinctive lozenge shape, valued for its rich nutrient profile as well as its economic and medicinal importance, making it a globally significant food commodity **[1, 2]**. The papaya plant exhibits three sex types: female, male, and hermaphrodite. Among these, hermaphrodite plants are often preferred for fruit production because every tree bears fruit [3,4]. In contrast, female papaya trees—though valued for their consistent flower production—require cross-pollination from male or hermaphrodite trees. Previous studies suggest that fruit flavor varies depending on the plant's sex [5]. However, conflicting reports exist regarding whether hermaphrodite or female plants produce sweeter fruit, leaving this question unresolved [6, 7].

Sweetness, a key indicator of ripeness, is linked to the accumulation of sucrose, glucose, and fructose, which fluctuate throughout the fruit's development and ripening stages, from immature green to fully mature [8]. Unlike some other fruits, papayas do not store starch during development; instead, sucrose accumulation is governed by the source-sink relationship between leaves (source) and fruit (sink), ultimately influencing sweetness, flavor, and overall quality [2]. Additionally, the spatiotemporal regulation of sugar-metabolizing enzymes—such as acid invertase (AI), sucrose phosphate synthase (SPS), and sucrose synthase (SuSy)-plays a critical role in sugar accumulation [2, 9]. Prior research indicates that papaya fruits exhibit low SPS and SuSy activity but high AI activity during growth and development [10]. In light of these factors, this study aims to conduct an organoleptic evaluation of female and hermaphrodite papaya fruits at three developmental stages to assess consumer preference. Furthermore, the temporal expression of sucrose-metabolizing enzymes (SPS, SuSy, and AI), along with biochemical analysis, will be explored to better understand the biochemical mechanisms underlying fruit quality and sweetness.

Given these factors, this study aims to conduct an organoleptic evaluation of female and hermaphrodite papaya fruits at three developmental stages to determine consumer preference. Investigate the temporal expression of sucrose-metabolizing enzymes (SPS, SuSy, and AI) alongside biochemical analysis to elucidate the mechanisms underlying fruit quality and sweetness.

As this study aims to clarify whether female or hermaphrodite papaya plants produce sweeter fruit by analyzing sugar metabolism and consumer preferences. The findings will help farmers optimize cultivation practices for better fruit quality and marketability, benefiting both agriculture and consumers. For the scientific community, this research provides deeper insights into the biochemical mechanisms of sugar accumulation in papaya, which could guide future breeding programs to enhance fruit sweetness and nutritional value. Ultimately, this work supports sustainable papaya production and improved food quality.

Materials and Methods

Sampe collection

Fruits from hermaphrodite and female papaya plants at three ripening stages (mature, intermediate, and green) were collected from three fields in Karachi: the Baseline Research Center (BARC) Experimental Field (University of Karachi), Memon Goth Papaya Farm, and Malir Papaya Farm. After transport to the lab, seeds and peels were removed, and the pericarp was diced, flash-frozen in liquid nitrogen, and stored at –80°C.

Physical analysis

Fruits were washed with distilled water, air-dried at room temperature on blotter paper, and measured for length, weight, and diameter.

Seed analysis

Seeds from both hermaphrodite and female papaya plant types at three maturity stage were soaked overnight to remove the sarcotesta (gelatinous membrane), then analyzed for color, shape, length, diameter, number, and fresh weight.

Sensory evaluation

Peeled and sliced fruits were evaluated by 30 panelists from University of Karachi and KIBGE, a research institute) for color (flesh and peel), firmness, aroma, flavor, and overall acceptability on a 1–5 scale (1 = least satisfactory, 5 = extremely satisfactory).

Total protein

Total protein extraction was performed by homogenizing 100 mg of fruit tissue in 2 mL of QB buffer [11]. The homogenate was centrifuged at 12,000 rpm for 15 min at 4°C to obtain a clear supernatant. Protein concentration was determined using the Bradford assay [12] with slight modifications, using bovine serum albumin as the standard.

Reducing sugar extraction and quantification

Frozen pulp samples (100 mg) were cryogenically pulverized and homogenized in 5 mL of 80% (v/v) aqueous ethanol. Following centrifugation at 9,000 rpm for 15 min at 4°C, the ethanolic supernatant was carefully transferred to fresh polypropylene tubes. Reducing sugar content was determined spectrophotometrically using the 3,5-dinitrosalicylic acid (DNS) method [13], with glucose serving as the calibration standard.

Total carbohydrate analysis

Total carbohydrate content was determined using a modified anthrone-sulfuric acid method [14]. Following the same extraction procedure as described for reducing sugars, the ethanolic extract was reacted with freshly prepared anthrone reagent (140 mg anthrone dissolved in 100 mL concentrated sulfuric acid). The mixture was heated at 100°C for 10 minutes to develop color, then cooled and measured spectrophotometrically at 620 nm. Glucose standards (0-100 μg/mL) were processed in parallel to generate a calibration curve for quantitative analysis.

Sugar metabolizing enzyme analysis

Sucrose phosphate synthase (SPS) and sucrose synthase (SuSy) activities were assayed using modified methods from [15]. Enzymes were extracted from plant samples using Mops-NaOH (pH 7.5) buffer, and homogenates were centrifuged at 14,000g for 20 minutes. Sucrose phosphate activity was measured using the anthrone-sulfuric method, with freshly isolated enzymes. The assay medium contained de-ionized water, extracted enzyme, and Mops-NaOH, incubated at 37°C for 15 minutes. The reaction was terminated with KOH and heated at 100°C, followed by the addition of anthrone reagent and incubation at 100°C for 20 minutes. The color developed was measured at A620 nm.

Sucrose synthase (SuSy) activity was measured similarly, using 4 mM fructose instead of Glc 6-P and fructose 6-P. Acid invertase (AI) activity was measured using [16] with slight modifications. The reaction mixture contained 4% sucrose solution and 1 M acetate buffer (pH 5.4), incubated at 37°C for 60 minutes. After adding DNSA reagent, the mixture was incubated at 100°C for 10 minutes, cooled, and absorbance recorded at A540 nm.

Statistical analysis

All experimental data were subjected to analysis of variance (ANOVA) using SPSS Statistics 23. Statistical significance was established at $p < 0.05$.

Results

Morphological analysis of fruit

The physical parameters of fruit, including weight, length, and diameter, were measured for female and hermaphrodite papaya plants at three stages of maturity. The results indicate that the fruit from female plants is spherical in shape, whereas the fruit from hermaphrodite plants is cylindrical or pear-shaped. Statistical analysis revealed significant differences ($p < 0.05$) in average fruit weight and length between the female and hermaphrodite plants at all three stages (green, intermediate, and mature). However, no significant differences ($p > 0.05$) were observed in the circumference of the fruits from both plant types (Table 1).

The seed length and diameter in both hermaphrodite and female papaya fruits remained relatively consistent across all three stages (green, intermediate, and mature). Seed length ranged from 0.4 cm to 0.6 cm, and seed diameter ranged from 0.16 cm to 0.46 cm. Additionally, some hermaphrodite papaya fruits were found to be seedless (Table 2). As the fruit matured, the seed color transitioned from white to brown or black. Both types of papaya seeds were covered with a transparent, gelatinous covering. Seed shapes varied considerably, including irregular, oblong, oval, and round forms. Significant variability in seed numbers was observed, with the female plant's fruit containing between 8 and 2,165 seeds, while the hermaphrodite plant's fruit contained between 12 and 561 seeds.

Table 1. Morphological characteristics of fruits from hermaphrodite and female papaya plants at different phenological stages

Fruit characteristics	Plant type	Green	Intermediate	Mature	PT	GS
Fruit weight (gm)	♀	121.53±2.4	527.63±0.86	367.33±2.8	***	***
	⚥	64.56±3.7	134.73±1.43	153.73±2.2		
Fruit length (cm)	♀	7.4±0.3	13.96±0.6	13.46±0.4	***	***
	⚥	8.93±1	8.63±0.4	12.26±1.42		
Fruit diameter (cm)	♀	8.03±1.3	9.22±0.7	8.55±0.3	ns	***
	⚥	4.36±0.1	5.56±0.5	13.66±1.97		

Hermaphrodite plant ⚥, Female plant (♀), (n=9), ns = non-significant *, **, *** = significant at $P < 0.05$, 0.01 and 0.001

Table 2. Morphological characteristics of seeds from hermaphrodite and female papaya plants at different phenological stages

Seed characteristics	Plant type	Green	Intermediate	Mature
Seed length (cm)	♀	0.35	0.6	0.7
	⚥	0.4	0.5	0.52
Seed diameter (cm)	♀	0.2	0.4	0.46
	⚥	0.31	0.35	0.36
Seed color	♀	white	brown	brown
	⚥	white	white	dark brown
Seed shape	♀	oblong	oblong	oblong
	⚥	irregular	oval	oblong
Seed number	♀	902	358	367
	⚥	112.33	240	216.66
Seed fresh weight (gm)	♀	10.47	47.37	27.94
	⚥	2.69	7.32	11.87

Hermaphrodite plant fruit ⚥, Female plant fruit ♀. (n=9)

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Sensory analysis
The ortho-nasal and retro-nasal odor profiles of papaya fruit samples from both plant types at three different maturity stages are shown in (Fig. 1 & Table 3). The results indicated that sensory attributes, including the color of the fruit's external surface, pulp color, aroma, taste, sweetness, and firmness, all increased as the fruit matured in both hermaphrodite and female papaya plants. Visual appearance analysis revealed that fruit flesh color, peel color, and firmness did not differ significantly ($p > 0.05$) between the two plant types at any of the maturity stages. However, the aroma and flavor of fruits from female papaya plants were rated more favorably by the appraisers, with a significant difference observed ($p < 0.05$). Overall, fruits from the female papaya plants were more highly accepted by the panelists. Sensory profiling also highlighted that the degree of maturity and ripeness had a significant impact on consumer preference and overall sensory qualities.

Table 3. Lexicon for organoleptic descriptive profiling of female and hermaphrodite papaya fruits at different ripening stages

Score	Fruit Skin Color	Fruit Flesh Color	Aroma	Firmness	Flavor	Overall acceptability
1			Aroma Less	Extremely Firm	Insipid	Undesirable
2			Pungent	Very Firm	Slightly Sweet	Less Acceptable
3			Woody	Firm	Sweet	Acceptable
4			Sweet	Slightly Firm	Less Sweet	Good
5			Fruity	Soft	Very Sweet	Excellent

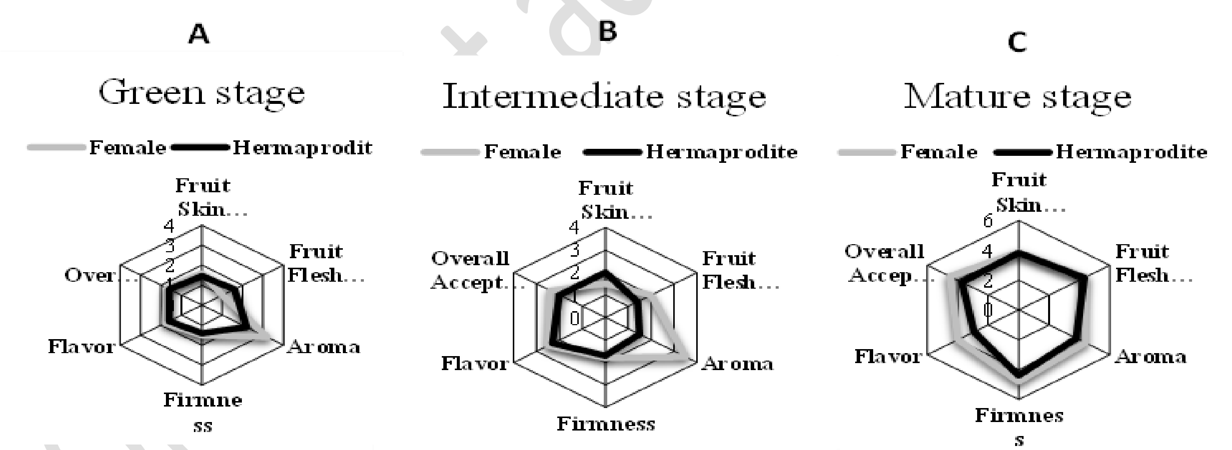


Figure 1. Sensory analysis of fruit skin color, flesh color, aroma, firmness, flavor, and overall acceptability of female and hermaphrodite papaya fruits at (A) Green stage, (B) Intermediate stage, and (C) Mature stage

Biochemical analysis
Statistical analysis revealed significant differences ($p<0.05$) in total proteins, reducing sugars, and carbohydrate contents between female and hermaphrodite papaya fruits at different growth stages. The highest total protein concentration was observed in the ripened fruit of the female plant (86.61 mg/g FW), while the lowest was found in the early growth stage of the hermaphrodite plant

fruit (49.01 mg/g FW). For reducing sugars and carbohydrate contents, both types of papaya plants exhibited a similar pattern, with a marked increase at the mature stage compared to the green stage (Fig. 2).

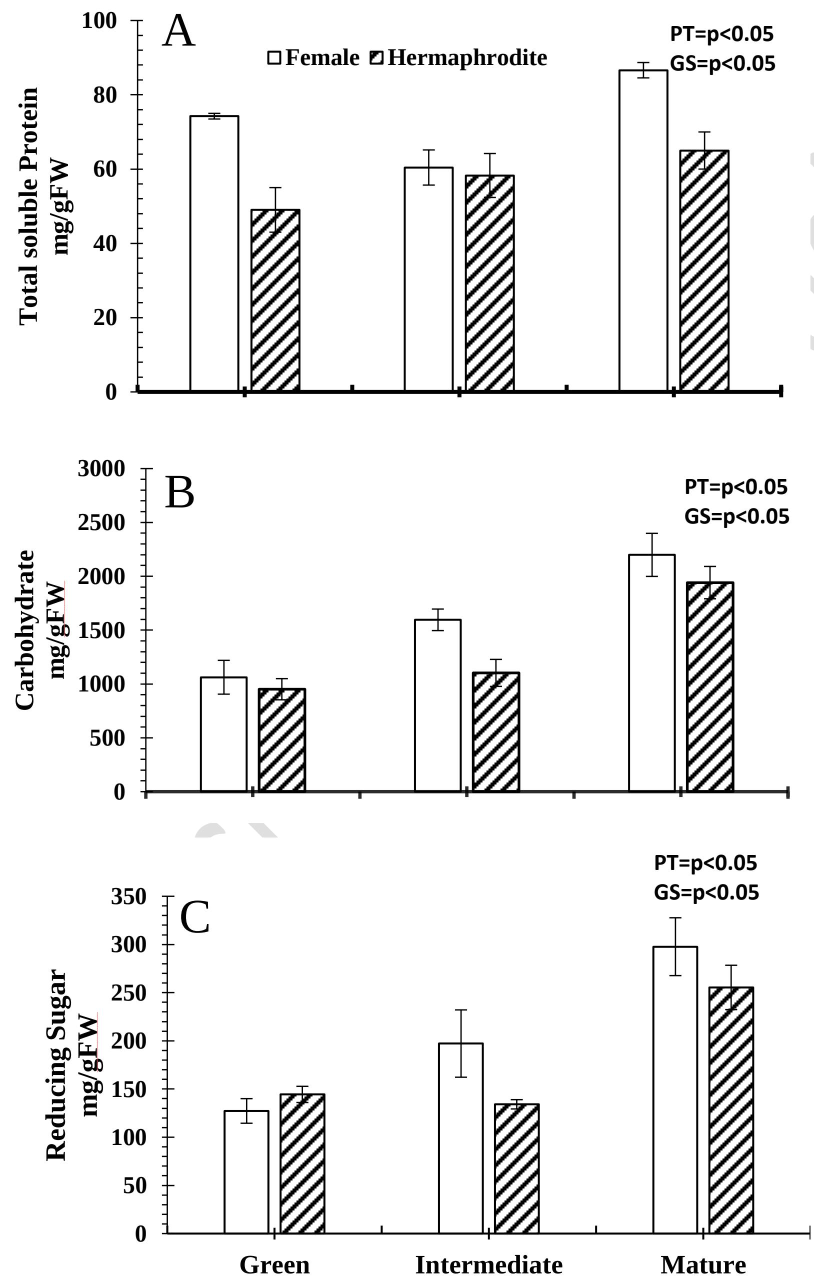
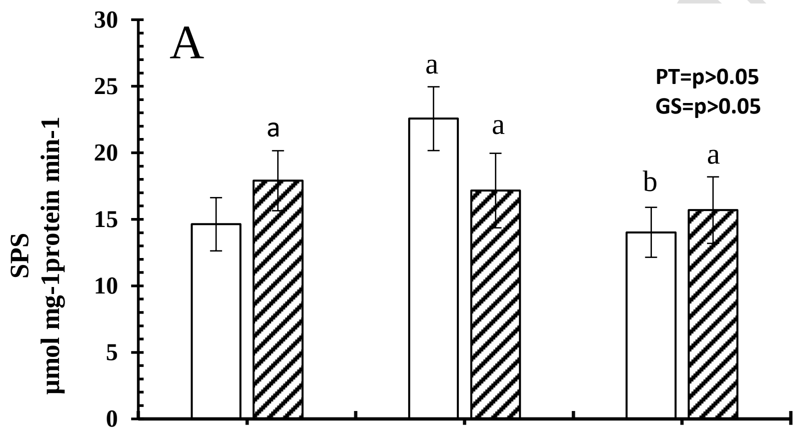
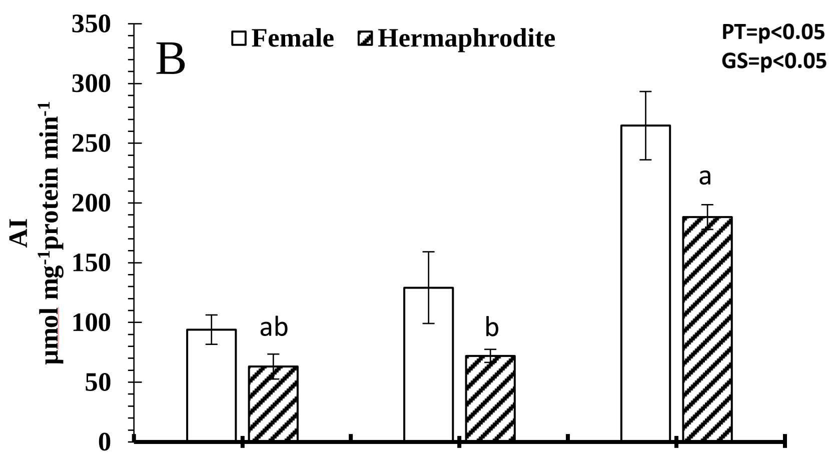


Figure 2. Biochemical analysis of female and hermaphrodite papaya fruits during three growth stages (A) Total soluble protein (B) Carbohydrate (C) Reducing sugar. Error bars represent mean ± SEM of three replicates

Sugar metabolizing enzymes analysis

Statistical analysis showed significant differences ($p<0.05$) in the activities of acid acid invertase (AI) and sucrose synthase (SuSy), while the activity of sucrose phosphate synthase (SPS) showed no significant difference ($p>0.05$) between the fruits of female and hermaphrodite papaya plants at three growth stages (green, intermediate, and mature). The highest AI activity was observed in the fruit of the female plant at the mature stage (264.72 µmol/mg protein/min), while the lowest activity was recorded in the green stage of the hermaphrodite plant (63.09 µmol/mg protein/min). Interestingly, AI activity was negatively correlated with SuSy activity. The highest SuSy activity was observed in the early stage of the female papaya fruit (17.76 µmol/mg protein/min), but it decreased as the fruit matured. Meanwhile, SPS activity remained low and relatively constant in both plant types with slight variation across growth stages (Fig. 3).





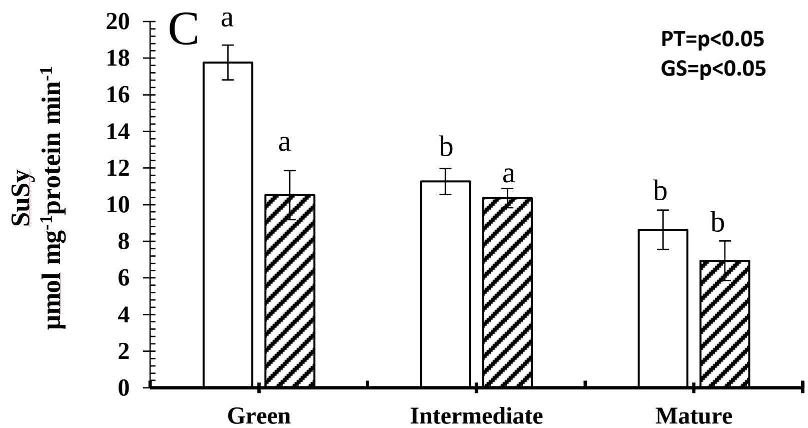


Figure 3. Comparative analysis of (A) Sucrose Phosphate Synthase (SPS) activity, (B) Acid Invertase (AI) activity, and (C) Sucrose Synthase (SuSy) activity in female and hermaphrodite papaya plant fruits at three different developmental stages. (Error bars represent the mean ± SEM of three replicates)

Table 4. Comparative profile of female and hermaphrodite papaya plants based on fruit physical parameters, sensory analysis, biochemical analysis, and sugar metabolizing enzymes analysis. (High ↑, Low ↓, and no difference −)

Analyses	Parameters	Fruit of female plant	Fruit of hermaphrodite plant
Morphological analysis	Fruit length (cm)	↑	↓
	Fruit diameter (cm)	↑	↓
	Fruit weight (gm)	-	-
Sensory analysis	Fruit skin color	-	-
	Fruit flesh color	-	-
	Aroma	↑	↓
	Firmness	-	-
	Flavor	↑	↓
	Overall acceptability	↑	↓
Biochemical analysis	Protein	↑	↓
	Carbohydrate	↑	↓
	Reducing sugar	↑	↓
Sugar metabolizing enzyme analysis	Sucrose phosphate synthase	-	-
	Sucrose synthase	↑	↓
	Acid invertase	↑	↓

Correlation analysis

The correlation analysis examined the relationship between carbohydrate and reducing sugar content and acid invertase enzyme activity at the ripening stage of both papaya plant types. In hermaphrodite papaya fruit, carbohydrate and reducing sugar content were inversely correlated with acid invertase activity. In contrast, in female papaya fruit, carbohydrate and reducing sugar content exhibited a significant positive correlation with acid invertase activity (Fig. 4).

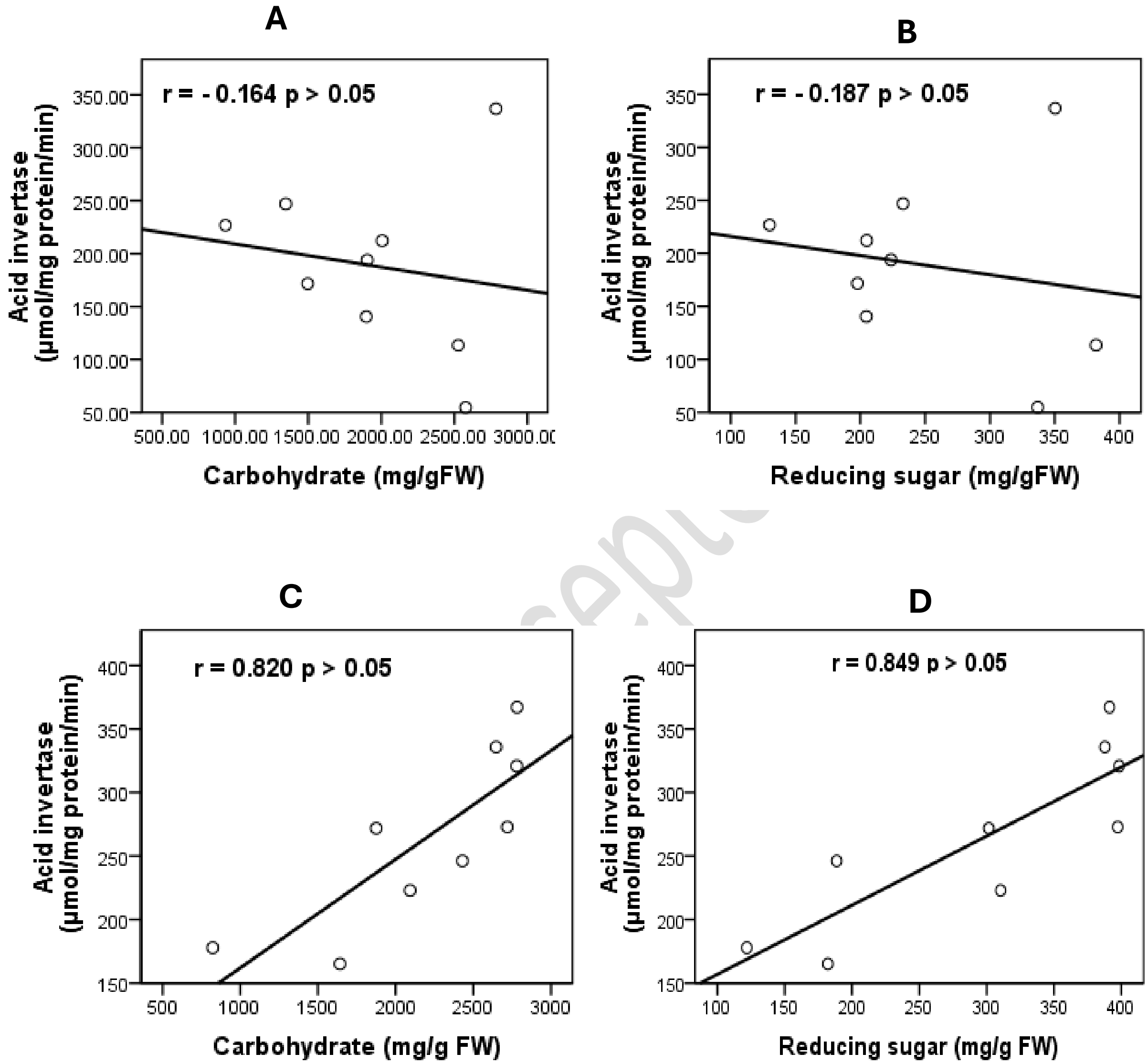


Figure 4. Pearson's correlation coefficient analysis of carbohydrate and reducing sugar attributed with Acid invertase activity of (A) female and (B) hermaphrodite papaya plant fruit at ripening stage

Discussion

Fruits from female papaya plants are typically round and large, while fruits from hermaphrodite plants are elongated and pear-shaped [17]. This morphological trait has also been observed by other researchers in both plant types [18, 19]. However, contradictory findings have been reported in some studies [20, 21]. Changes in the physical attributes of both plant types occur as the fruit reaches physiological maturity, with weight gain in papaya following a simple sigmoid curve [19].

Additionally, the appearance of papaya fruits is a sex-related trait linked to the flower's form [22].

Sensory evaluation indicated that both the pulp and peel color of the fruit changed with ripening [23]. Furthermore, panelists rated the flavor, aroma, and overall acceptability of female papaya fruit more favorably across all ripening stages. These findings contradict previous studies [21, 24].

Protein content in papaya fruits was generally low, with hermaphrodite papaya fruit exhibiting lower total protein content compared to female papaya fruit. Protein content increased as the fruit approached physiological maturity, consistent with findings in other climacteric fruits [18]. Changes in protein content during fruit senescence indicate various metabolic activities, including the increased activity of enzymes such as cellulose and polygalacturonase, which support cell growth, pigment synthesis, and the breakdown of enzymes involved in fruit growth and ripening [25].

Papaya fruit sugars, including sucrose, fructose, and glucose, showed a significant increase in carbohydrate content during ripening, as observed in Indian papayas [27]. This increase is attributed to the conversion of sucrose and starch into glucose, which is subsequently used in respiration. At earlier stages, glucose is more abundant, but as fruit development progresses, sucrose accumulation significantly increases. The sugar content in papaya fruit is also influenced by the activity of sugar-metabolizing enzymes [28].

Sucrose inversion and starch degradation significantly affect the flavor and nutritional content of papaya fruit [8]. Biochemical conversions of carbohydrates are regulated by both antagonistic and synergistic mechanisms throughout fruit development [29]. Initially, glucose content is higher, but as the fruit matures, sucrose accumulation increases, surpassing glucose levels [30].

A substantial increase in acid invertase (AI) activity was observed during papaya fruit ripening, which aligns with the rate of carbon import [8]. Invertase is a key regulatory enzyme responsible for the hydrolysis of disaccharide sugars [31]. During the mature stage, the sugar content in the papaya mesocarp increased, reflecting strong regulation of invertase activity [9]. These observations are consistent with the accumulation of AI and its high activity during fruit ripening.

AI activity was significantly higher in female papaya fruit compared to hermaphrodite fruits, with AI levels increasing from the green to the ripened stage. This suggests that sucrose degradation and the subsequent formation of hexose sugars are more prominent in the ripening stages than in earlier stages [31]. These results were corroborated by the quantification of reducing sugars, which increased in both plant types during the ripening phase. High mesocarp sugar levels in the mature fruit further support the role of AI in sugar accumulation, consistent with findings in citrus fruits [9, 32].

Sucrose phosphate synthase (SPS) activity remained constant during papaya fruit development and ripening [10, 32]. However, no correlation was found between SPS activity and sugar levels in either type of papaya fruit across the growth stages.

Sucrose synthase (SuSy) is a critical enzyme in sucrose catabolism, playing a key role in the cleavage and resynthesis of sucrose. SuSy is involved in the transport of sucrose through various pathways, including storage, metabolic, and structural functions [8]. SuSy activity was higher during the green stage of fruit development but decreased as the fruit matured, consistent with findings from other studies [32].

In both female and hermaphrodite papaya fruits, SuSy activity was significant but negatively correlated with sugar accumulation during ripening. This suggests that sucrose import is more important than starch degradation in the mature stage **[33]**.

Correlation analysis revealed that, in female papaya fruit, increasing reducing sugars were positively correlated with AI activity during the final phase of fruit growth. This suggests that AI plays a significant role in sucrose accumulation **[32]**. However, in hermaphrodite papaya fruit, a negative correlation was observed between AI activity and total sugars at the mature stage. This result contradicts previous findings **[8]** but aligns with studies in other androdiecious plants **[34]**.

Conclusion

This study provides a comprehensive characterization of female and hermaphrodite papaya fruits at three different phenological stages, based on physical parameters, sensory profiling, biochemical analysis, and sugar-metabolizing enzyme activity. Sensory profiling revealed that fruits from female papaya plants were more acceptable at all stages. Sucrose synthase enzyme activity was crucial during the early stages of fruit development in both plant types, while acid invertase activity was prominent in mature fruits, correlating with sugar accumulation. Fruits from female plants exhibited higher AI activity in later stages and higher SuSy activity in earlier stages of development.

Authors' contributions

Execute the research: Z Riaz, help in data analysis: F Mehdi, S Sahar & N Afzal, Review and finalized the manuscript: I Jamil, Supervised the work: S Galani.

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