



Dynamic Transformations in Fruit Color, Bioactive Compounds, and Textural Characteristics of Purple-Fleshed Dragon Fruit (*Hylocereus costaricensis*) Across Fruit Developmental Stages Under Humid Tropical Climate

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Abstract: Purple-fleshed dragon fruit is gaining popularity worldwide due to its distinctive characteristics and health benefits. This climbing cactus, introduced to humid tropical climates, presents challenges in assessing fruit quality. The dynamic transformations in fruit color, bioactive compounds, and textural attributes across 11 developmental stages from 10 to 32 days after flowering under humid tropical conditions were studied. Color analysis revealed significant intensification of red-violet hues, with L* values decreasing by 14.74% and a* values increasing from -8.14 to 32.96. The color transformation is initiated in the pulp at 25 days and the peel at 27 days after flowering. Betalain synthesis commenced after 20 days with rapid accumulation between 25 and 32 days, correlating with color development. Antioxidant activity increased from 79.38% at 10 days to 86.76% at 20 days, followed by a steady decline. Phenolic content peaked at 121.40 mg gallic acid equivalent per 100 g at 25 days before declining, while the flavonoid content decreased with the advancement of fruit development. Concurrent reduction in peel thickness and fruit firmness was also observed. These findings show that purple-fleshed dragon fruit can adapt well to humid tropical conditions, with a 32-day developmental cycle, offering vital insights into quality and maturation phases.

Keywords: dragon fruit; fruit development; color values; hue angle; betalains; bioactive compounds; firmness; peel characters

1. Introduction

Dragon fruit, popularly known as Pitaya, is a climbing cactus belonging to the *Hy*locereus genus of the Cactaceae family. This genus comprises 16 species, primarily distinguished by their peel and pulp colors. The four most cultivated species [1] are (i) *Hylocereus* undatus (white-flesh with pink skin), (ii) *Hylocereus polyrhizus* (red-flesh with pink skin), (iii) *Hylocereus costaricensis* (purple-flesh and pink skin) and (iv) *Hylocereus (Selenicerus)* megalanthus (white-flesh with yellow skin) [2,3].

Dragon fruit is renowned for its anti-inflammatory, anti-spasmodic, and radioprotective effects [4] and antioxidant, anti-microbial, anti-cancer, and anti-diabetic activities [5]. This has led to growing global interest and expanding its cultivation into non-traditional areas with suitable climatic conditions. Although native to Central Mexico and South America [6], it is now successfully cultivated in South Asian tropical countries, including the Indian continent, which offers diverse agroclimatic conditions conducive to its growth [2].



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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). The fruit's ability to adapt to various growing conditions and its high economic return further contribute to its increasing popularity and economic value [7,8]. Among the various colored pitaya fruits, the dark pink/purple-fleshed species (*Hylocereus costaricensis*) has emerged as a particularly intriguing subject of study, owing to its attractive, vibrant color, unique exotic appearance, refreshing taste, and promising content of bioactive compounds, most notably betalains, which contribute to its distinctive coloration and antioxidant properties [9].

As a non-climacteric fruit, dragon fruit poses challenges in determining optimal harvest timing, necessitating precise evaluation to ensure fruit quality, consumer acceptance, and extended shelf life. The spectrum of color changes occurring in the fruit peel and pulp during growth and maturation is a critical indicator of fruit development [10] and is closely linked to consumer acceptance [11]. These visual cues are intricately associated with the underlying biochemical transformations, particularly the accumulation of bioactive compounds such as phenolics, flavonoids, and betalains. The metabolic profiles can vary significantly among cultivars, underscoring the necessity for cultivar-specific data in distinct climatic contexts [12]. Previous studies have emphasized the substantial impact of edaphoclimatic conditions on dragon fruit development, highlighting the necessity of region-specific investigations [13–16]. These findings underscore the importance of conducting region-specific investigations when introducing exotic crops into new environments to ensure optimal fruit quality and market acceptance.

The purple-fleshed dragon fruit (*Hylocereus costaricensis*) is a relatively recent introduction to humid tropical climates, where edaphoclimatic conditions potentially influence the fruit's developmental patterns, fruit and pulp color transition, bioactive compound accumulation, and overall quality. A comprehensive investigation of these transformations throughout the fruit's development will provide crucial information on its nutritional value, bioactive compounds, antioxidant capacity evolution, and color dynamics, which are essential for determining optimal harvest maturity to maximize health benefits. The betalain accumulation trajectory, closely linked to the fruit's signature purple-red pulp color, could serve as a visual maturity indicator.

Understanding the changes in bioactive compounds also supports the fruit's potential applications in functional foods and as a natural colorant source. Hence, this study aims to comprehensively examine the dynamic changes in fruit and pulp color, bioactive compounds, and fruit physical and textural attributes of purple-fleshed dragon fruit grown in humid tropical climates. By tracking transformations from early fruit growth to full maturity, we seek to provide insights into fruit maturation stages, potential quality indicators, and adaptation to new environmental conditions.

2. Materials and Methods

2.1. Experimental Site

Fruits from three-year-old, purple-fleshed dragon fruit (*Hylocereus costaricensis*), planted on a single-pole system (four plants per pole) at 10×9 feet spacing and which started flowering 15 months after planting, were used for the study. The fruit species identification was confirmed based on a comprehensive morphological characterization method [3,17]. The commercial orchard was located in the Thiruvananthapuram district of the Kerala state, India, situated at 8°39′18.5″ N latitude, 76°57′43.2″ E longitude, and an altitude of 177 m above mean sea level. The climate of the site is humid tropical, with an average annual rainfall of 1665 mm with 74–90% relative humidity. The yearly temperature ranged from 24 °C to 31 °C, with 7–8 h of sunshine during the summer. The fruits were collected and analyzed at various growth and development stages at 5 day intervals, starting from 10 days after flowering (DF) until 25 DF (10, 15, 20, 25 DF). After 25 DF, daily observations were recorded (26, 27, 28, 29, 30, 31, and 32 DF) due to rapid changes in peel and pulp color and other physico-chemical attributes. The experiment period was limited to 32 DF due to the onset of fruit splitting. The flowers were labeled individually with metallic tags on the day of flowering to track their developmental stages. The study was conducted from May

2023 to June 2024. At each growth stage, the fruits were hand-harvested in the morning at their respective growth stages, and fifteen fruits as replicates were used to analyze the fruit characteristics.

2.2. Fruit Weight Estimation

Fruit weight was determined by weighing the individual fruits with a top pan electronic weighing balance (CyberlabTM, capacity 600 g, accuracy 0.01 g) and expressed in gram [13].

2.3. Fruit and Pulp Color Estimation

The color of dragon fruit and pulp during the various maturation stages was quantified using a Hunter-Lab Colorimeter (Lovibond, The Tintometer Group, Salisbury, UK). The color was assessed based on the L*, a*, and b* parameters [18], and the color values were expressed as CIE Lab* coordinates where L* denotes Lightness (scaled from 0 for black to 100 for white), a* represents redness (positive values indicate redness, while negative values indicate greenness), and b* indicates yellowness (positive values indicate yellowness, while negative values indicate blueness). Fruit color measurements were recorded in triplicate for each fruit from the fruit's middle section, excluding bracts, and averaged for accuracy. Pulp color values were recorded from the middle of longitudinally cut halves of each fruit. The determination of color intensity, chroma (C*), and hue angle (hue°) were further computed from CIE a*b* values. Chroma (C*) was calculated using the formula C* = $(a^2 + b^2)^{1/2}$, and hue angle (hue°) that provides insights into color perception by consumers was calculated using the formula hue° = tan¹ (b/a) [19].

2.4. Betalain Estimation

The betalains content in dragon fruit samples was estimated using the spectrophotometric method [20]. The fruit sample (1 g) was homogenized with 10 mL of distilled water, centrifuged, and the supernatant was diluted. The absorbance of the diluted aqueous extract was measured at 538 nm using a spectrophotometer. Total betalains content was calculated using the formula: Total betalains content (mg betacyanin equivalent per 100 g⁻¹ FW) = (A × 535 × 10 × DF × 1000)/(60,000 × 1 × 1) × 100, where A is the absorbance at 538 nm, DF is the dilution factor, and 535 and 60,000 are the molecular weight and molar extinction coefficient of betacyanin, respectively. Results were expressed as mg betacyanin equivalents per 100 g (mg BE 100 g⁻¹) fresh weight of dragon fruit.

2.5. Antioxidant Activity Estimation

The total antioxidant activity of the dragon fruit samples was assessed via a DPPH (2,2-diphenyl-1-picrylhydrazyl) radical scavenging assay [21]. Fruit samples were extracted (1:10 w/v) in 80% methanol, and extract aliquots were reacted with DPPH solution (1:2 v/v). Absorbance measurements at 517 nm following 30 min dark incubation were used to calculate the inhibition percentage.

2.6. Phenol Estimation

The dragon fruit sample (1 g) was extracted with 10 mL of 80% ethanol, followed by centrifugation. The supernatant was collected, the residue was re-extracted with 5 mL of 80% ethanol, centrifuged again, and the resulting supernatants were combined. The pooled supernatant was evaporated using a water bath. The dried residue was dissolved in 5 mL of distilled water, and a 200 μ L aliquot of this solution was used to estimate the total phenol content using the Folin-Ciocalteau spectrophotometric method [22]. Absorbance was measured at 760 nm against a reagent blank. The phenol content was calculated by comparing the sample's absorbance with a standard curve plotted using varying concentrations of gallic acid, and the results were expressed as mg of gallic acid equivalents (GAE) per gram of fresh weight of the fruit sample (mg GAE 100 g⁻¹).

2.7. Flavonoid Estimation

The total flavonoid content of the dragon fruit pulp was determined using the aluminum chloride colorimetric method [23]. The dragon fruit sample was extracted as per the procedure outlined for phenol estimation (Section 2.6). From the extracted solution, 200 μ L aliquot was taken for analysis. The absorbance of the reaction mixture was measured at 510 nm against a blank using a spectrophotometer (Systronics (India) Ltd., Gujarat, India). The flavonoid content was calculated by plotting a standard curve with absorbance values from different concentrations of quercetin and were expressed as milligrams of quercetin equivalent (mg QE) per 100 g of the fruit (mg QE 100 g⁻¹).

2.8. Fruit Firmness and Pulp Firmness

The fruit and pulp firmness of individual fruits at different developmental stages were evaluated using a texture analyzer (TA. HD plus, Stable Microsystems, Godalming, Surrey, UK) as per the procedure outlined by American Society of Agricultural Engineers (ASAE) Standards [24], with some modifications. A 2.5 mm stainless steel needle (P/2N) probe was used to puncture the fruits, and the required pressure was measured and expressed in kg cm⁻². To determine fruit firmness, the whole fruit and pulp firmness and the fruit without peel were analyzed at three equidistant points on the radial axis to ensure standardized and precise firmness measurement across different stages of development.

2.9. Estimation of Fruit Peel Characteristics

Peel thickness and peel percentage were analyzed to determine the fruit peel characteristics. Peel thickness was measured using a Vernier Caliper (Mitutoyo Corporation, Kawasaki, Kanagawa, Japan 150 mm, resolution 0.02 mm) to record thickness in millimeters [13]. Measurements were taken at different growth and developmental stages to capture changes in peel thickness over time. Peel percentage, representing the proportion of peel weight relative to total fruit weight, was calculated as Peel (%) = (Peel weight/Fruit weight) × 100 [13] to provide insights into the relative contribution of peel in the overall fruit structure.

2.10. Statistical Analysis

The experiment employed a completely randomized design (CRD) with growth stages (10, 15, 20, 25, 26, 27, 28, 29, 30, 31, and 32 days after flowering [DF]) as treatments, each with 15 replications. Data were subjected to analysis of variance (ANOVA), and treatment means were compared using Fisher's Protected Least Significant Difference (LSD) test at p < 0.05. Critical Difference (CD) values were calculated for pairwise comparisons between treatment means. Linear relationships between measured parameters were evaluated using Pearson correlation coefficients (r) at p < 0.05. All statistical analyses, including ANOVA and correlation computations, were performed using R 4.4.2 version software with the grapesAgri1 package [25].

3. Results

3.1. Fruit Weight

Fruit weight of purple-fleshed dragon fruit (*Hylocereus costaricensis*) exhibited significant variations across different developmental stages from 10 to 32 days after flowering (DF) (Table 1). The initial fruit weight at 10 DF was 167.51 g, which progressively increased throughout the developmental period. A substantial increment in fruit weight was observed between 20 and 25 DF, where the weight increased from 212.28 g to 255.30 g, representing a 20.3% increase during this five-day interval. As evident from Table 1, the most rapid phase of weight accumulation occurred between 25 and 27 DF, during which the fruit weight increased from 255.30 g to 312.83 g, demonstrating a 22.5% increase in just two days. After 27 DF, the rate of weight gain gradually decreased, although it continued to show statistically significant differences between successive stages (p < 0.05). The progressive weight gain reflected the fruit's active growth phase, and the highest percentage increase observed between 25 and 27 DF indicated the critical stage of fruit development. The final fruit weight recorded at 32 DF was 370.16 g, representing a total increase of 120.9% from the initial weight at 10 DF.

DF	Fruit Weight (g)	Fruit Color			Pulp Color				
		L*	a*	b*	C*	L*	a*	b*	C*
10	167.51 ± 6.70 k	42.46 ± 1.22 d	$-8.14\pm0.73~\text{g}$	15.76 ± 1.03 ab	$17.74\pm0.88~\text{ef}$	$92.85 \pm 0.72^{\ b}$	$1.20\pm0.12\text{g}$	13.19 ± 0.73 ^b	$13.24\pm0.88\ f$
15	185.47 ± 8.84 j	42.92 ± 1.14 cd	-7.5 ± 0.74 fg	15.89 ± 1.14 ab	$17.57 \pm 0.58 \text{ ef}$	96.04 ± 0.74 ^a	2.09 ± 0.31 f	19.46 ± 0.74 ^a	19.57 ± 0.74 ^e
20	$212.28 \pm 8.15 \ i$	$43.75 \pm 1.34 \ ^{\rm c}$	$-7.87 \pm 0.68 \ {\rm fg}$	15.22 ± 1.34 ^a	$17.13 \pm 0.73 \ {\rm fg}$	57.83 ± 0.68 ^c	$3.46 \pm 0.35 \ ^{e}$	2.39 ± 0.68 ^c	$4.21 \pm 0.35 \ d$
25	255.30 ± 7.72 h	45.86 ± 1.20 b	-8.11 ± 0.30 f	16.03 ± 1.18 b	17.96 ± 0.74 ^e	40.78 ± 0.62 d	15.89 ± 0.58 d	-6.6 ± 0.63 g	17.21 ± 0.73 ^c
26	$283.32 \pm 3.66 \ g$	48.00 ± 1.18 ^a	-8.56 ± 0.58 f	14.46 ± 1.20 ^c	$16.80\pm0.58~\mathrm{g}$	27.00 ± 0.58 ^e	26.63 ± 0.73 ^c	-7.72 ± 0.74 h	27.73 ± 0.58 b
27	312.83 ± 4.17 f	39.19 ± 1.02 ^e	10.41 ± 0.65 ^e	11.57 ± 1.02 d	15.56 ± 0.88 h	22.53 ± 0.66 f	27.01 ± 0.88 ^c	-5.47 ± 0.65 f	27.56 ± 1.08 b
28	$335.76 \pm 3.78 \ ^{\rm e}$	37.73 ± 1.03 f	20.05 ± 0.74 d	$7.79 \pm 0.72^{\ e}$	21.51 ± 0.74 d	22.44 ± 0.58 f	29.43 ± 1.32 b	-5.44 ± 1.08 f	29.93 ± 1.32 ^a
29	348.23 ± 4.46 d	37.59 ± 1.10 f	25.08 ± 1.08 ^c	$7.65\pm0.64~^{\rm e}$	$26.22 \pm 1.08 \ c$	$21.75\pm0.62~\text{g}$	$29.64\pm1.08~a$	$-4.43 \pm 1.37 {\rm e}$	$29.97 \pm 1.33 \ a$
30	357.17 ± 9.16 ^c	37.43 ± 1.32 f	29.16 ± 1.32 b	6.93 ± 0.68 f	29.97 ± 1.32 b	$21.30\pm0.68~\text{g}$	30.19 ± 0.74 ab	-4.37 ± 0.58 ^e	30.50 ± 1.52 ^a
31	363.61 ± 8.35 b	$37.14 \pm 1.35 \text{ a}$	$32.83 \pm 1.37 \ a$	$4.65\pm0.63~\text{g}$	33.16 ± 1.52 ^a	20.19 ± 0.74 h	30.10 ± 1.52 ab	-4.47 ± 1.32 ^e	30.43 ± 0.74 ^a
32	$370.16 \pm 7.58 \ ^{a}$	$36.20 \pm 1.10\ ^{a}$	$32.96 \pm 1.06 \ ^{a}$	$4.42\pm0.48g$	$33.26 \pm 0.74 \ ^{a}$	$20.25\pm0.72\ h$	$30.08\pm1.42\ ab$	$-2.8\pm0.64\ d$	$30.21 \pm 1.42 \ ^{a}$
SE (±m)	1.78	0.31	0.24	0.26	0.24	0.17	0.24	0.24	0.38
CD (0.05)	4.98	0.86	0.66	0.71	0.67	0.48	0.68	0.66	0.75

Table 1. Changes in fruit and pulp color in purple-fleshed dragon fruit during fruit maturation.

Different letters in the column for each parameter denote significant differences among treatments at p < 0.05, as per the Least Significant Difference (LSD) test.

3.2. Fruit Color

The color parameters of *H. costaricensis* fruit demonstrated a complex transformation during fruit development (Table 1). The L* value, a metric quantifying light reflectance, provides insight into color tones, with higher values indicating lighter shades and lower values representing darker tones. In this study, the fruit's L* values exhibited a non-linear progression: an initial increase from 42.46 at 10 DF to a peak of 48.00 at 26 DF, followed by a progressive decline to 36.20 at 32 DF (Table 1). The reduction in L* values starting at 27 DF marked the onset of pigmentation and transition of color from green (light shades) to red (darker shades) (Figure 1). Further reduction in L* value during later developmental stages reflected the progression of pigmentation.



Figure 1. Changes in fruit peel and flesh color in purple-fleshed dragon fruit during fruit maturation.

The a* values, which reflect the shift from green (negative) to red (positive) values, significantly increased throughout fruit growth and maturation stages. The a* values increased from -8.14 at 10 DF to 32.96 at 32 DF (Table 1), and a notable transition from negative to positive occurred between 26 DF (-8.56) and 27 DF (10.41), indicating the critical point when the fruit color shifted from green to red. This red pigmentation continued to intensify until maturity. In contrast, the b* values of the fruit, which indicate the transition from yellow (+) to blue (-), exhibited a decreasing trend from 15.76 at 10 DF to 4.42 at 32 DF. Meanwhile, the chroma values representing color intensity and purity increased from 17.74 at 10 DF to 33.26 at 32 DF (Table 1), indicating greater intensity and purity of the color as the fruit matured. The comprehensive analysis of the above fruit color parameters revealed a progressive reduction in light reflection, the transition from green to red coloration, and a shift from yellow to blue tones, with the first appearance of color on the fruit occurring at 27 DF (Figure 1), followed by progression of pigmentation, intensification of color, and the emergence of a purplish-red hue, providing a visual representation of the fruit's maturation trajectory.

3.3. Pulp Color

The assessment of pulp color parameters in purple-fleshed dragon fruit illustrated a progressive change from creamy white to purple during fruit growth and maturation. The L* value of the pulp exhibited a substantial decline, decreasing from 92.85 at 10 days after flowering (DF) to 20.25 at 32 DF (Table 1). A marked reduction in pulp L* values was evident between 15 and 25 DF, signifying a loss of luminosity during the fruit's maturation phase, with the purple color becoming distinctly visible at 25 DF, as depicted in Figure 1.

In contrast to L* values, the a* values, representing the intensity of redness, exhibited a significant increase, rising from 1.2 at 10 DF to 30.08 at 32 DF (Table 1), indicating a pronounced intensification of red coloration during maturation. The most substantial relative change in a* values, coupled with the sharp reduction in L* values, occurred between 20 and 25 DF. This period represented a critical point marking the transition from whiteness to redness in the fruit pulp (Figure 1).

The b* values representing yellowness demonstrated a declining trend throughout the maturation process. The values were initially positive up to 20 DF (2.39) and became negative at 25 DF (-6.60) (Table 1), reflecting a shift from yellow to darker tones. Additionally, the C* values, which indicate color intensity, increased from 17.74 at 10 DF to 30.21 at 32 DF (Table 1). This reflected the intensification and progression of pulp pigmentation. The hue angle (hue°), which indicates the color's position on a 360° color wheel, also displayed remarkable changes, with hue° decreasing consistently throughout the growth and maturation stages.

The comprehensive analysis of pulp color parameters illustrated a progressive chromatic transformation from creamy white to purple, characterized by a substantial decline in lightness, significant intensification of redness, a shift from yellow to blue tones, and a consistent reduction in hue angle. This revealed the complex color evolution during fruit maturation from 10 to 32 days of flowering, with the first visible appearance of purple color at 25 DF (Figure 1).

Overall, the analysis of fruit and pulp color parameters (L*, a*, b*, C*, and hue°) indicated a clear transition in color characteristics. There was a noticeable decrease in L* (luminosity), b* (yellowness), and hue° values, alongside an increase in a* (redness) and C* (color intensity) values. This transition demonstrated the evolution of the fruit's color from green to a purplish-red hue and the transition of pulp color from creamy white to purple during the maturation stages. Importantly, the color changes in the pulp were observed earlier than in the fruit, occurring at 25 DF compared to 27 DF for the fruit (Figure 1).

3.4. Betalain

The betalains synthesis and accumulation in purple-fleshed dragon fruit revealed a distinct developmental pattern throughout fruit maturation (Table 2). During the early

stages of fruit development (10–20 DF), the betalains content was undetectable. The initial betalains synthesis was observed at 25 DF (0.86 mg BE 100 g⁻¹), and the highest accumulation occurred between 25 and 26 DF, where levels rose from 0.86 to 5.08 mg BE 100 g⁻¹. This rapid accumulation continued with an 85.43% increase from 26 to 27 DF (9.41 mg BE 100 g⁻¹), followed by a 34.58% increase from 28 DF (10.56 mg BE 100 g⁻¹) to 29 DF (14.21 mg BE 100 g⁻¹), and a final 7.31% increase to reach peak content at 30 DF (15.25 BE 100 g⁻¹). After reaching this maximum, a slight decline of 8.46% was observed in the final stages (31–32 DF), with values stabilizing around 14 mg BE 100 g⁻¹ (14.12 and 13.96 mg BE 100 g⁻¹, respectively). This progressive accumulation of betalains was accompanied by visible changes in pulp coloration, transitioning from creamy white to purple, reflecting the fruit's maturation (Figure 1). The period between 25 DF and 30 DF represented the critical phase of pigment synthesis in *H. costaricensis*, characterized by intense betalains buildup that reflected the fruit's maturation process. Statistical analysis revealed significant differences (*p* < 0.05) between developmental stages, except for measurements at 31 and 32 DF.

Table 2. Changes in fruit weight, betalains, and total phenol and flavonoids in purple-fleshed dragon fruit during fruit maturation.

DF	Betalains (mg BE 100 g $^{-1}$)	Antioxidant Activity (%)	Total Phenol (mg GAE 100 g $^{-1}$)	Total Flavonoids (mg QE 100 g ⁻¹)
10	0	$79.38\pm1.77~^{\rm d}$	116.95 \pm 1.58 $^{\rm c}$	$85.07\pm3.33~^{\rm a}$
15	0	$84.45\pm1.14~^{\rm b}$	120.13 ± 0.93 ^b	$84.82\pm3.83~^{\rm a}$
20	0	86.76 ± 1.20 ^a	111.48 ± 1.16 ^d	83.28 ± 3.20 ^{ab}
25	0.86 ± 0.12 $^{ m g}$	82.75 ± 1.68 ^c	$121.40\pm1.18~^{\rm a}$	$81.48 \pm 3.30 \ ^{ m b}$
26	5.08 ± 0.31 f	76.36 \pm 1.63 $^{ m e}$	$94.98\pm0.83~^{\rm e}$	$57.89\pm4.86~^{\rm c}$
27	9.42 ± 0.32 $^{ m e}$	70.28 ± 0.99 f	$93.40 \pm 1.52~{ m f}$	53.79 ± 4.26 ^d
28	10.56 ± 0.30 ^d	69.49 ± 1.84 $^{ m f}$	$88.68 \pm 0.93~{ m g}$	52.25 ± 4.71 ^d
29	14.21 ± 0.37 ^b	$69.26\pm1.10~^{ m f}$	86.32 ± 0.79 h	52.00 ± 4.02 $^{ m d}$
30	15.25 ± 0.30 a	$62.30 \pm 1.31~{ m g}$	$82.31\pm0.81^{\rm ~i}$	51.23 ± 3.48 ^d
31	14.12 ± 0.26 ^{bc}	53.99 ± 1.90 ^h	$78.72 \pm 1.09^{\ j}$	45.84 ± 4.93 $^{ m e}$
32	13.96 ± 0.28 ^c	$50.83\pm1.37~^{ m i}$	$72.71\pm0.09~^{\rm k}$	$39.43 \pm 3.90~^{\rm f}$
SE (±m)	0.06	0.38	0.29	1.04
CD (0.05)	0.18	1.07	0.80	2.91

Different letters in the column for each parameter denote significant differences among treatments with a standard deviation of p < 0.05, as per the Least Significant Difference (LSD).

3.5. Antioxidant Activity

Antioxidant activity, measured by DPPH radical scavenging, demonstrated a bellshaped pattern with an initial increase from 79.38% at 10 DF to 86.76% at 20 DF, followed by a steady decline through the later stages of fruit development. (Table 2). The maximum free radical scavenging activity recorded at 20 DF represented an optimal point in fruit development for antioxidant capacity. The most pronounced decrease occurred between 25 and 26 DF, where values dropped from 76.36 to 70.28%. The activity stabilized temporarily between 27 and 29 DF, maintaining values between 69 and 70%, before continuing to decline. By 32 DF, the antioxidant activity had reached its lowest point at 50.83%, representing a 41.4% reduction from the peak value observed at 20 DF. Statistical analysis revealed significant differences (p < 0.05) between developmental stages, except during the stabilization period of 27–29 DF.

3.6. Phenol

Total phenolic compounds in purple-fleshed dragon fruit exhibited a biphasic distribution pattern during fruit development (Table 2). The initial phenol content was substantial at 10 DF (116.95 \pm 1.58 mg GAE 100 g⁻¹), which fluctuated during early development before attaining its maximum concentration at 25 DF (121.40 mg GAE 100 g⁻¹). Notably, two distinct phases were observed: an early accumulation phase (10–25 DF) characterized by elevated phenolic levels above 110 mg GAE 100 g⁻¹ and a subsequent reduction phase (26–32 DF). The transition point occurred at 26 DF, where phenolic content decreased sharply by 21.8% to 94.98 mg GAE 100 g⁻¹. This marked the beginning of a systematic reduction in phenolic compounds throughout the remaining developmental period. The rate of decline was particularly evident between 26 and 28 DF, where levels decreased from 94.98 to 88.68 mg GAE 100 g⁻¹. By the final developmental stage (32 DF), the phenolic content had diminished to 72.71 mg GAE 100 g⁻¹, representing a 40.1% reduction from the peak value at 25 DF.

3.7. Flavonoid

Analysis of total flavonoid content in purple-fleshed dragon fruit revealed a distinctive pattern during fruit development. The flavonoid levels were highest during early developmental stages (85.07 mg QE 100 g⁻¹ at 10 DF) and maintained relatively stable concentrations until 25 DF (81.48 mg QE 100 g⁻¹), followed by a sharp decline of 28.95% between 25 and 26 DF, decreasing to 57.89 mg QE 100 g⁻¹. Subsequently, flavonoid content decreased gradually, stabilizing between 27 and 30 DF (ranging from 53.79 to 51.23 mg QE 100 g⁻¹). The final developmental stages (31–32 DF) showed a further reduction, reaching the lowest concentration of 39.43 mg QE 100 g⁻¹ at 32 DF, representing a total decrease of 53.65% from initial levels (Table 2).

3.8. Fruit and Pulp Firmness

The firmness of the fruit and pulp revealed distinct patterns during development. Fruit firmness exhibited a bi-phasic trend, initially increasing from 2.09 kg cm⁻² at 10 DF to a peak at 3.98 kg cm⁻² at 20 DF, followed by a progressive decline. A sharp decrease was observed between 28 and 29 DF, where firmness dropped to 0.54 kg cm⁻², remaining stable until 31 DF, and decreased without significance to 0.45 at 32 DF (Table 3). In contrast, pulp firmness showed a consistent declining pattern throughout the development, decreasing from 1.16 kg cm⁻² at 10 DF to 0.17 kg cm⁻² at 32 DF, representing a reduction of 85.34% in firmness (Table 3).

Table 3. Changes in fruit and pulp firmness, peel thickness, and peel percentage in purple-fleshed dragon fruit during fruit maturation.

DF	Fruit Firmness (kg cm ⁻²)	Pulp Firmness (kg cm ⁻²)	Fruit Peel Thickness (mm)	Peel Percentage (%)
10	$2.09\pm0.10~^{d}$	1.16 ± 0.012 a	7.30 ± 0.03 $^{\rm a}$	68.42 ± 2.93 $^{\rm a}$
15	$3.88 \pm 0.10^{\ \mathrm{b}}$	$0.98 \pm 0.010^{\ \mathrm{b}}$	6.40 ± 0.03 ^b	67.01 ± 3.54 ^a
20	$3.98\pm0.09~^{\rm a}$	$0.97\pm0.011~^{\rm c}$	6.30 ± 0.03 ^{bc}	63.01 ± 2.82 ^b
25	$3.37\pm0.06~^{\rm c}$	0.69 ± 0.009 ^d	6.20 ± 0.03 ^{bc}	60.01 ± 2.98 $^{\rm c}$
26	$3.37\pm0.06~^{\rm e}$	$0.54\pm0.010~^{\rm e}$	6.0 ± 0.07 ^c	52.21 ± 1.34 ^d
27	$3.37\pm0.06~^{\rm f}$	$0.29 \pm 0.005~{\rm f}$	5.20 ± 0.03 ^d	$46.73\pm2.07~^{\mathrm{e}}$
28	$3.37\pm0.06~^{\rm g}$	0.26 ± 0.006 g	$4.00\pm0.03~^{\rm e}$	$36.20\pm2.0~^{\rm f}$
29	0.54 ± 0.05 ^h	0.25 ± 0.006 ^h	3.50 ± 0.03 f	$28.20 \pm 2.17~^{ m g}$
30	0.54 ± 0.05 h	$0.24\pm0.005^{\text{ i}}$	$3.00\pm0.05~^{g}$	$26.20\pm1.89~^{\rm h}$
31	0.54 ± 0.05 h	0.20 ± 0.005 ^j	$2.50\pm0.04^{\text{ h}}$	$23.22\pm2.47^{\text{ i}}$
32	0.45 ± 0.10 h	$0.17\pm0.009~^{\rm k}$	$2.20\pm0.04~^{\rm i}$	$18.18 \pm 2.10^{\ j}$
SE (±m)	0.017	0.002	0.010	0.636
CD (0.05)	0.049	0.006	0.028	1.778

Different letters in the column for each parameter denote significant differences among treatments with a standard deviation of p < 0.05, as per the Least Significant Difference (LSD) test.

3.9. Fruit Peel Characteristics

The peel thickness and peel percentage of the purple-fleshed dragon fruit decreased significantly throughout fruit development. The peel thickness reduced from 7.30 mm at 10 DF to 2.20 mm at 32 DF, while the peel percentage reduced from 68.42% to 18.18% during the same period (Table 3). These changes represent total reductions of 69.86%

in peel thickness and 73.43% in peel percentage. The most substantial decrease in both measurements occurred between 28 DF and 29 DF, which coincides with the fruit's full-color development stage, indicating a key maturation period.

3.10. Correlation Analysis

The correlation analysis of fruit quality parameters in purple-fleshed dragon fruit using the Pearson correlation coefficient (Figure 2) illustrates a complex interplay of physical and chemical characteristics during fruit development. Among the 171 simple correlations analyzed, 155 parameters were significant at the $p \leq 0.05$ significance level. Based on the degree of intensity of the correlations, 73.01% of the analyzed correlations were strong to very strong, 22.81% were of average intensity, and 4.06% were low intensity. These results emphasize the reliability of the present findings and suggest that the fruit quality parameters studied are highly interrelated with complex relationships among the variables.



Figure 2. Correlation coefficients (r) and the probability levels of fruit and pulp color parameters (L*, a*, b* C* and hue°), fruit and pulp firmness, peel thickness, peel percentage betalains, fruit weight, phenol, and flavonoids of purple-fleshed dragon fruit during fruit maturation at $p \le 0.05$ significance level.

Days after flowering (DF) emerged as a crucial factor, strongly correlating with multiple parameters: it has strong positive correlations with fruit weight (0.962 ***), peel a* values (0.78 **), pulp a* values (0.937 ***), and betalains (0.897 **), while negatively correlating with pulp L* values (-0.964 ***), pulp firmness (-0.954 ***), and peel percentage (-0.879 ***). This indicates that as the fruit matures, it gains weight, develops color (especially in the red spectrum), becomes softer, and accumulates pigments. Peel and pulp color parameters (L*, a*, b*, C*, hue°) correlate strongly with other fruit characteristics. The strong correlation between peel a* values and betalains (0.954 ***) provides a potential non-destructive method for estimating bioactive compound content. The fruit and pulp firmness showed a strong correlation (0.853 ***) and were negatively correlated with DF, indicating consistent softening throughout ripening. Peel thickness and peel percentage strongly correlated (0.987 ***); both decreased with DF, suggesting peel thinning during maturation. Notably, betalains, phenols, and flavonoids exhibited strong correlations with each other and various physical parameters, with betalains strongly correlating with DF (0.897 **) and fruit weight (0.978 ***). These findings have significant implications for planning the harvest maturity and quality assessment. The strong correlations between easily measurable physical characteristics (such as color and firmness) and chemical composition suggest potential for developing quick, non-destructive methods for assessing fruit maturity and quality.

4. Discussion

Assessment of the fruit development in purple-fleshed dragon fruit revealed a 32-day development stage, with fruit exhibiting a steady increase in fruit weight from 167.51 g at 10 days after flowering (DF) to a peak of 370.16 g by 32 DF, marking a 121% increase (Figure 3A). This substantial growth trajectory aligns with studies on both red-fleshed [13,16] and white-fleshed dragon fruit types [26], suggesting a common developmental trend across different cultivars. Several physiological processes contribute to this growth pattern, with early stages characterized by cell differentiation and enlargement [27], accompanied by the accumulation of water, sugars, and other solutes, significantly contributing to fruit weight gain [28]. While the general pattern is consistent across dragon fruit species, cultivar-specific variations exist due to genetic differences [29]. The present study recorded the highest percentage increase in fruit weight (39.89%) between 25 DF and 30 DF, representing a critical developmental stage unique to purple-fleshed dragon fruit. This interplay between genetic factors and humid tropical climatic conditions underscores the complex nature of fruit development in purple-fleshed dragon fruit, highlighting the need for cultivar-specific management practices to optimize fruit quality and yield.



Figure 3. Changes in (**A**) Fruit weight, (**B**) Betalains, (**C**) Antioxidant activity, (**D**) Phenol, and (**E**) Flavonoids in purple-fleshed dragon fruit during fruit maturation.

The color parameters of purple-fleshed dragon fruit undergo significant changes during maturation, reflecting complex physiological processes. Initially, the fruit L* value increased from 42.46 at 10 DF to a peak of 48.00 at 26 DF (Figure 4A), indicating a brighter, lighter color in the early stages. However, it subsequently decreased to 36.20 by 32 DF as

pigmentation intensified. This reduction in L* during later stages marked the development of the fruit's characteristic purplish-red color. The observed transition from green to redviolet hues, characterized by decreasing L* values, aligns with findings in red [13] and white pitaya [30], where similar reductions in L* values correspond with increasing pigmentation during fruit maturation. This pattern demonstrates the consistent relationship between L* value changes and fruit ripening across pitaya varieties.



Figure 4. Changes in fruit color parameters: (**A**) Lightness (L*), (**B**) Redness (a*), (**C**) Yellowness (b*), (**D**) Chroma (C*), and (**E**) Hue values (hue[°]) in purple-fleshed dragon fruit during fruit maturation.

Concurrently, the fruit a* values increased substantially from -8.14 at 10 DF to 32.96 at 32 DF, with a notable transition from green to red occurring between 26 DF (-8.56) and 27 DF (10.41) (Figure 4B), signaling the onset and progressive intensification of red pigmentation until full maturity. Similar trends in a* values based on the degree of maturity were observed in red [26] and white-fleshed [31] dragon fruit. Simultaneously, the b* values steadily declined from 15.76 at 10 DF to 4.42 at 32 DF (Figure 4C), indicating reduced yellow pigmentation during maturation. This aligns with the findings by Ortiz and Takahashi [31] in white-fleshed dragon fruit and by Lata et al. [30] in red-fleshed dragon fruit grown under humid tropical climatic conditions. Meanwhile, Magalhaes et al. [16] observed similar declining trends with variations in maturation timings. These consistent changes in b* values throughout fruit growth and maturation are linked to the degradation of chlorophyll and carotenoid pigments [32] and the formation of betalains [14,33].

The chroma values (C*) of purple-fleshed dragon fruit increased from 17.74 at 10 DF to 33.26 at 32 DF (Figure 4D), denoting an increase in color intensity throughout the maturation stages. The observed increase in C* values aligns with the findings of Ortiz and Takahashi [31] and Magalhaes et al. [16], who observed a linear increase in C* values in *H. undatus*. These results underscore the steady pattern of increasing color intensity during the maturation stages of dragon fruit.

The analysis of fruit pulp color parameters in purple-fleshed dragon fruit also revealed a progressive change in the pulp color during maturation. The pulp L* values decreased significantly throughout the development stages, ranging from 92.85 at 10 days after flowering (DF) to 20.25 at 32 DF, with a marked reduction between 15 and 25 DF (Figure 5A). In red pitaya, this reduction happened between 25 and 30 DF (Phebe et al. [15]). The decrease in L* values reflects increased pulp pigmentation due to the interconversion of pigments [13,16]. In this study, seed maturation also played a crucial role in pulp color development (Figure 1), and the development of seeds contributed to reduced pulp L* values [34]. As the seed color became darker in the purple-fleshed dragon fruit, the pulp L* values decreased, revealing a significant relationship between the onset of pigmentation and seed maturation. The fruit pulp pigmentation initially began around the seeds at 25 DF, following the complete blackening of the seeds. This sequence of pulp color development about seed maturation aligns with the findings by Jamaludin et al. [26] in *H. polyrhizus*. Overall, these results suggest that the development of pulp color in dragon fruit is closely linked to seed maturation and pigment interconversion, highlighting notable variations across different species and stages of fruit development.



Figure 5. Changes in pulp color parameters: (**A**) Lightness (L*), (**B**) Redness (a*), (C) Yellowness (b*), (**D**) Chroma (C*), and (**E**) Hue values (hue[°]) in purple-fleshed dragon fruit during fruit maturation.

The a* values of the purple-fleshed dragon fruit pulp showed a substantial increase from 1.2 at 10 days after flowering (DF) to 30.08 at 32 DF, indicating an intensification of coloration as the fruit matured. The most pronounced changes in a* values occurred between 20 and 25 DF (Figure 5B) and coincided with a sharp decrease in L* values. This shift reflects a loss of whiteness and a progression of redness in the pulp, consistent with findings in red-fleshed dragon fruits, which exhibit substantial variations in a* values based on the degree of maturity [26]. Likewise, Ortiz and Takahashi [31] documented a steady increase in a* values for white-fleshed dragon fruit. Collectively, these collective findings reinforce that the pattern of color development varies among different dragon fruit species and growing conditions.

The pulp b* values exhibited a decreasing trend (Figure 5C), aligning with observations by Singh et al. [13] in red-fleshed dragon fruit grown under Indian semi-arid conditions. Furthermore, the pulp color intensity values (C*) exhibited significant fluctuations with quadratic behavior (Figure 5D). The C* values increased from 17.74 at 10 DF to 19.57 at 20 DF, then decreased to 4.21 at 25 DF before rising again to 30.21 at 32 DF (Table 1). This pattern of an initial decrease followed by an increase in pulp C* values of purple-fleshed dragon fruit grown under humid tropical conditions was in agreement with the findings of Singh et al. [13] in red-fleshed dragon fruit grown in semi-arid conditions. Similar trends were reported by Jamaludin et al. [26] in red-fleshed dragon fruits in Malaysia across seven growth and development stages. In the current study, the highest perceptible change in color intensity and purity (C* values) was observed at 25 DF, indicating the onset of pulp pigmentation. The fruit pulp attained full purplish-red color 28 days after flowering

(Figure 1). This observation was consistent with the findings of Phebe et al. [15] in red dragon fruit, further confirming that the timing of color intensity expression can vary depending on species and growing conditions.

The hue° values of the fruit decreased significantly, dropping below 30° at 28 DF and reaching 8° at 32 DF (Figure 5E). Ortiz and Takahashi [31] documented a similar reduction in hue° for white-fleshed dragon fruit, which decreased from 118° at 21 DF to 10° at 32 DF in Brazil. The reduction in the hue° observed in the purplish-red dragon fruit in the current study suggests a color transition from green to red during fruit development, which corroborates observations by Jamaludin et al. [26] in red dragon fruit and by Magalhaes et al. [16] in white-fleshed dragon fruit. The decreasing hue° values, as the fruit color shifts from green to red, signify physiological maturity, with mature fruits typically exhibiting hue° values below 30° [31,35]. In this study, the hue angle of purplish-red dragon fruit reached below 30° at 28 DF, indicating the readiness for harvest maturity. The intensity of red fruit color and days after flowering is a key indicator of maturity and fruit quality in dragon fruit [11]. A study conducted by Van To et al. [36] in Vietnam confirmed that fruits with a hue° equal to or less than 30° were suitable for marketing, further emphasizing the importance of hue° as a maturity and quality indicator for dragon fruit.

Overall analysis of fruit and pulp color parameters (L*, a*, b*, C*, and hue°) of purplish red dragon fruit demonstrated a clear transition from green to a purplish-red hue throughout the fruit growth and development stages. This color transformation from lighter and less intense colors to darker and more intense colors during fruit maturation is in agreement with the findings of Ortiz and Takahashi [31] in white-fleshed dragon fruit and by Singh et al. [13] in red-fleshed dragon fruit. The change in fruit color of *H. undatus* occurred between 28 and 30 DF under Vietnam conditions [26], while under Mexican climatic conditions, it occurred at 25 DF [37] and between 28 and 29 DF in Brazil [31]. In red-fleshed fruits grown in a humid tropical climate, color change was observed at 26 DF [30]. In Malaysia, this change occurred at 25 DF [26] and between 26 and 27 DF [15], while it was observed later at 30 DF [13] under semi-arid conditions. In the present study, however, the onset of pigmentation occurred at 27 DF, with color intensity and purity steadily increasing until the end of the evaluation period of 32 DF.

Notably, the color changes in the fruit and pulp of purple-fleshed dragon fruits were not synchronized; pigmentation appeared earlier in the pulp (at 25 DF) than in the fruit (at 27 DF) (Figure 1). Although the onset of pigmentation varied, a similar report of asynchronous color development in the fruit and pulp was observed in red-fleshed dragon fruit [13]. These patterns of color change emphasize the significant impact of climatic factors on the maturation timeline of dragon fruit across different regions.

The color development in dragon fruit is closely linked to the synthesis of betalains [38] and the fading of green color due to a marked decrease in chlorophyll [33]. In purple-fleshed dragon fruit, the betalain synthesis was initiated at 25 DF with minimal content (0.86 mg BE 100 g^{-1}). The most substantial increase in betalain accumulation occurred between 25 and 26 DF (Figure 3B), with a remarkable 490.70% increase. This accumulation trend continued throughout the maturation phase till 30 DF, after which it decreased slightly. This rapid accumulation of betalains coincided with the visible transition in pulp color, particularly between 25 DF and 30 (Figure 1). This trend is consistent with the linear increase in betalain content during growth stages, as reported by Singh et al. [13] and Zitha et al. [32] in H. polyrhizus. It corroborates the findings of Junior et al. [33] in H. undatus. The absence of betalains in the early stages (10–20 DF) further supports the notion that betalains synthesis occurs later during fruit development. The slight decline in betalain content (8.46%) after 30 DF suggests a stabilization phase in its biosynthesis, which contrasts with previous studies and may be due to cultivar-specific or environmental influences [12]. This underscores the importance of growing conditions on betalain accumulation and color intensity during fruit maturation. This unique pattern highlighted the regulation of betalain biosynthesis and its relationship with color development in both the fruit peel and pulp, as well as other aspects of maturation in purple-fleshed dragon fruit.

The decline in antioxidant activity, measured by DPPH radical scavenging activity from 86.76% to 50.97% during fruit development, reveals a complex pattern of antioxidant metabolism. The observed antioxidant activity pattern aligns with studies by Zitha et al. [32] and is further contextualized by recent biochemical investigations. Arivalagan et al. [20] highlighted the dynamic nature of biochemical transformations in the Hylo*cereus* species, demonstrating that antioxidant capacity is a function of complex metabolic processes during fruit development. The peak antioxidant activity at 20 days after flowering (86.76%) (Figure 3C) represents a critical phase of metabolic optimization. Singh et al. [13] corroborated this observation in red-fleshed dragon fruit, noting significant physiochemical changes during fruit development. These transformations suggest a nuanced interplay of biochemical mechanisms that influence antioxidant properties. The substantial reduction in radical scavenging activity, particularly the sharp decline between 25 and 26 days after flowering, indicates significant biochemical transitions such as metabolic reprogramming, alterations in enzymatic activities, and transformations in secondary metabolite composition. The temporary stabilization of antioxidant activity between 27 and 29 days after flowering suggests a potential adaptive metabolic response during fruit development, a phenomenon observed across various fruit species. By 32 days after flowering, the 41.4% reduction in antioxidant capacity underscores the dynamic nature of fruit biochemistry. This pattern highlights the critical window for harvesting to preserve optimal nutritional quality, as emphasized by Jiang et al. [6]. The statistically significant variations between developmental stages emphasize the complex biochemical transitions occurring during fruit maturation, with potential implications for fruit physiology, defense mechanisms, and nutritional value.

The total phenolic content in the purple-fleshed dragon fruit flesh exhibited a more complex, non-linear pattern with notable fluctuations throughout development. Initially, the phenolic content increased from 116.95 mg GAE 100 g^{-1} at 10 DF to 121.40 mg GAE 100 g⁻¹ at 25 DF and then decreased to 72.71 mg GAE 100 g⁻¹ at 32 DF, representing a 35.15% decrease (Figure 3D). This versatile pattern suggests that the biosynthesis and accumulation of phenolic compounds, which contribute to the fruit's antioxidant capacity and color, are tightly regulated by multiple factors during fruit development. The initial increase in phenolic content may be attributed to the fruit's defense mechanism against oxidative stress during early growth stages. At the same time, the subsequent decrease could result from either dilution effects as the fruit increases in size or the conversion of phenolics into other metabolites. This pattern of phenolic compounds peaking before full maturity and then declining towards the over-maturation phase in the present study is supported by Kahkonen et al. [39]. However, Zitha et al. [32] reported a continuous increase in total phenolic content with fruit development, contrasting with the present study, which highlights the role of environmental factors in influencing phenolic biosynthesis. These fluctuations underscore the intricate nature of phenolic accumulation and the versatile patterns of secondary metabolite production in purple-fleshed dragon fruit grown in humid tropical climates, where environmental conditions significantly influence the fruit's biochemical pathways.

Similarly, the flavonoid content of the purple-fleshed dragon fruit revealed a complex developmental pattern characterized by high initial concentrations followed by a systematic decline throughout fruit maturation. Maintaining high flavonoid levels (85.07 to 81.48 mg QE 100 g⁻¹) during early development (10–25 DF) suggests an active phase of flavonoid biosynthesis during initial fruit growth. However, the sharp decline (28.95%) observed between 25 and 26 DF (Figure 3E) represents a critical transition point in fruit development, signaling a significant shift in the secondary metabolite profile. The subsequent gradual decrease and stabilization of flavonoid levels between 27 and 30 DF (53.79 to 51.23 mg QE 100 g⁻¹), followed by a further reduction to 39.43 mg QE 100 g⁻¹ at 32 DF, coincided with other developmental events. This decline could be attributed to the conversion of flavonoids into other metabolites or a reduction in biosynthesis as the fruit shifts its resources towards other compounds, like sugars, during the later stages of development [17,18].

Fruit firmness is a critical determinant of palatability, acceptability, and commercial acceptance of most fruits and vegetables. The decline in the firmness of fruit and pulp and peel thickness affects eating quality and post-harvest shelf life. In purple-fleshed dragon fruit, the fruit firmness is initially increased up to 20 days after flowering (DF). Before decreasing consistently until the full-color development stage (29 DF) (Figure 6A), with no further significant changes in firmness. The initial increase in the fruit's firmness could be due to the active growth phase, which involves the proliferation of fruit cells [40]. In contrast to fruit firmness, pulp firmness decreased steadily throughout development, dropping from 1.159 kg cm⁻² at 10 DF to 0.169 kg cm⁻² at 32 DF (Figure 6B), with the fruit becoming much softer by the end of the evaluation period (32 DF). Firmness stabilization was observed around 29 DF (Figure 6B), suggesting optimal maturity. Studies on whitefleshed dragon fruits grown in Thailand found firmness stabilization at 33 days [41], while under Malaysian conditions, it occurred at 28 days [14] and 40 DF for red-fleshed dragon fruit grown under semi-arid climate [13]. This decrease in firmness is often associated with the increased levels of water-soluble pectin resulting from the breakdown of pectin components and cell wall degradation caused by hydrolytic enzymes [42].



Figure 6. Changes in (**A**) Fruit firmness, (**B**) Pulp firmness, (**C**) Peel thickness, and (**D**) Peel percentage in purple-fleshed dragon fruit during fruit maturation.

Peel characteristics, such as thickness and peel percentage, are important factors in determining harvest maturity and post-harvest shelf life. Maintaining optimal peel characteristics is vital for preserving the marketability, shelf life, and overall quality of dragon fruits [35]. In this study, on purple-fleshed dragon fruit, as the fruit matured and developed color, there was a corresponding reduction in peel thickness and percentage. Peel thickness significantly reduced from 0.73 mm at 10 DF to 0.22 mm at 32 DF (Figure 6C), while peel percentage decreased from 68.42% (10 DF) to 18.18% (32 DF) (Figure 6D). The most substantial decrease in both peel content and peel thickness occurred between 28 DF and 29 DF, aligning with the stage of full-color development. Analogous patterns have been reported in white-fleshed and red-fleshed dragon fruit studies [14,31,33]. Magalhaes et al. [16] reported that skin thickness decreased linearly with maturation, with a maximum thickness of 9.15 mm obtained at 28 days after flowering and a reduction to 2.96 mm at 48 days in white-fleshed dragon fruit. Similarly, Ortiz and Takahashi [31] observed a decrease in skin thickness from 10.6 mm at 21 days to 1.17 mm at 32 days after flowering. Junior et al. [33] noted a reduction in peel thickness from 11.14 (7 DF) to 3.44 mm (42 days) with advancing ripeness in H. undatus, whereas, in red-fleshed dragon fruit, Singh et al. [13] reported a declining trend in peel thickness from 20 DF until 45 DF.

The correlation revealed valuable perspectives into the fruit development process, depicting a clear picture of the ripening progression. The data suggests a highly coordinated process where changes in physical characteristics are closely linked to biochemical changes. The strong correlations between color parameters in both the peel and pulp indicate synchronized changes in pigmentation throughout the fruit. The physical attributes were found to correlate with increased redness [13]. The consistent negative correlations between firmness and DF and positive correlations with peel thickness indicated a softening of the fruit and thinning of the peel during ripening, likely reflecting cell wall breakdown and water loss. The accumulation of betalains, phenols, and flavonoids during ripening indicated increased antioxidant capacity and potential health benefits as the fruit matures. Significantly, the strong correlations between easily measurable parameters (like color or firmness) and chemical composition suggest that these physical traits can be reliable indicators of fruit maturity and quality [43].

5. Conclusions

This comprehensive study on the developmental processes of purple-fleshed dragon fruit (Hylocereus costaricensis) development in humid tropical conditions is the first line of work to understand the developmental mechanism, pigment accumulation patterns, and bioactive compound synthesis. The research identified a critical rapid growth phase between 25 and 32 days after flowering, characterized by significant changes in color, biochemical, and physical attributes. The study highlighted asynchronous color transitions between fruit and pulp, with the pulp exhibiting an earlier color shift at 25 days after flowering, followed by the fruit peel at 27 days after flowering. The pulp color transitioned from creamy white to purplish-red, while the fruit peel shifted from green to purplish-red hues, coinciding with the rapid accumulation of betalains. Fruit development from 10 to 32 days after flowering recorded a 121% total increase in fruit weight and a marked decrease in peel thickness (69.86%), peel percentage (73.43%), pulp firmness (85.34%), and fruit firmness (78.47%). A reduction in antioxidant activity (37.97%), phenolic content (37.83%), and flavonoids (53.65%) were also recorded with the advancement of fruit development. The correlation analysis between color transitions, synthesis of bioactive compounds, and other fruit characteristics revealed that these parameters are interconnected and serve as valuable indicators of fruit maturity and quality, emphasizing the multifaceted nature of dragon fruit maturation.

Interestingly, the developmental timeline of this species in humid tropical climates was shorter compared to red-fleshed varieties grown in semi-arid conditions. The identified key fruit developmental stages, color changes, and bioactive compound profiles highlight the complex interplay between various physiological processes during dragon fruit development and underscore the species' adaptation to humid tropical climatic conditions. These findings will be crucial for addressing fruit management, quality, and harvesting of purple-fleshed dragon fruit grown in humid tropical locations worldwide.

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References

- 1. Ortiz-Hernandez, Y.D.; Carilli, J.A.S. Pitahaya (Hylocereus spp.): Short Review. Commun. Sci. 2012, 3, 220–237.
- Wakchaure, G.C.; Kumar, S.; Meena, K.K.; Rane, J.; Pathak, H. Dragon Fruit Cultivation in India: Scope, Constraints and Policy Issues. *Tech. Bull.* 2021, 27, 47.
- 3. Abirami, K.; Swain, S.; Baskaran, V.; Venkatesan, K.; Sakthivel, K.; Bommayasamy, N. Distinguishing Three Dragon Fruit (*Hylocereus* spp.) Species Grown in Andaman and Nicobar Islands of India Using Morphological, Biochemical, and Molecular Traits. *Sci. Rep.* **2021**, *11*, 2894. [CrossRef] [PubMed]
- 4. Kaur, G.; Thawkar, B.; Dubey, S.; Jadhav, P. Pharmacological Potentials of Betalains. J. Complement Integr. Med. 2018, 15, 20170063. [CrossRef]
- 5. Joshi, M.; Prabhakar, B. Phytoconstituents and Pharmaco-Therapeutic Benefits of Pitaya: A Wonder Fruit. *J. Food Biochem.* 2020, 44, 13260. [CrossRef]
- 6. Jiang, Y.; Qu, H.; Zhou, L.; Yang, M.; Yang, Y.; Niu, L. Advances in Understanding the Fruit Development and Ripening Processes of Dragon Fruit (*Hylocereus* spp.). *Sci. Hortic.* **2020**, *265*, 109218.
- Thaiudom, S.; Oonsivilai, R.; Thaiwong, N. Production of Colorant Powder from Dragon Fruit (*Hylocerecus polyrhizus*) Peel: Bioactivity, Heavy Metal Contamination, Antimutagenicity, and Antioxidation Aspects. J. Food Process. Preserv. 2021, 45, e15044. [CrossRef]
- 8. Jalgaonkar, K.; Mahawar, M.K.; Bhushan Bibwe, B.; Kannaujia, P. Postharvest Profile, Processing and Waste Utilization of Dragon Fruit (*Hylocereus* spp.): A Review. *Food Rev. Int.* **2020**, *38*, 733–759. [CrossRef]
- 9. Perween, T.; Mandal, K.K.; Hasan, M.A. Dragon Fruit: An Exotic Super Future Fruit of India. *J. Pharmacogn. Phytochem.* 2018, 7, 1022–1026.
- 10. Lichtenzveig, J.; Noy, S.; Zilberstaine, M. The Inheritance of White Versus Red Fruit Flesh Color in Pitaya (*Hylocereus undatus*). *Hort Sci.* **2000**, *35*, 1317–1318.
- 11. Wakchaure, G.C.; Choudhari, J.D.; Kukde, R.B.; Reddy, K.S. Postharvest technology of dragon fruit. Tech. Bull. 2023, 41, 45.
- 12. Wu, Y.; Xu, J.; He, Y.; Shi, M.; Han, X.; Li, W.; Zhang, X.; Wen, X. Metabolic profiling of pitaya (*Hylocereus polyrhizus*) during fruit development and maturation. *Molecules* **2019**, *24*, 1114. [CrossRef] [PubMed]
- 13. Singh, A.; Swami, S.; Panwar, N.R.; Kumar, M.; Shukla, A.K.; Rouphael, Y.; Sabatino, L.K.P. Development changes in the physicochemical composition and mineral profile of red-fleshed dragon fruit grown under semi-arid conditions. *Agronomy* **2022**, *12*, 355. [CrossRef]
- 14. Ortiz, T.A.; Takahashi, L.S.A. Pitaya fruit quality (*Hylocereus undatus* [Haworth] Britton & Rose) according to physiological maturity. A review. *Rev. Colomb. Cienc. Hortic.* **2020**, *14*, 63–75.
- 15. Phebe, D.; Chew, M.K.; Suraini, A.A.; Lai, O.M.; Janna, O.A. Red-fleshed pitaya (*Hylocereus polyrhizus*) fruit colour and betacyanin content depend on maturity. *Int. Food Res. J.* 2009, *16*, 233–242.
- 16. Magalhaes, D.S.; Ramos, J.D.; Pio, L.A.S.; Boas, E.V.D.B.V.; Pasqual, M.; Rodrigues, F.A.; Rufini, J.C.M.; dos Santos, V.A. Physical and physicochemical modifications of white-fleshed pitaya throughout its development. *Sci. Hortic.* **2019**, *243*, 537–543. [CrossRef]
- 17. Sethunath, K.; Bhaskar, J. Evaluation of diversity in dragon fruit (*Hylocereus* spp.) genotypes grown in Kerala, India. *J. Appl. Hortic.* **2024**, *26*, 127–131.
- 18. Archana, R.; Rani, C.I.; Geetha, P.; Amuthaselvi, G.; Muthuvel, I.; Neelavathi, R. Value addition in dragon fruit and evaluation of the products (*Hylocereus costaricensis*). *Biol. Forum Int. J.* **2023**, *15*, 180–186.
- 19. Siddiq, M.; Iezzoni, A.; Khan, A.; Breen, P.; Sebolt, A.M.; Dolan, K.D.; Ravi, R. Characterisation of new tart cherry (Prunus cerasus L.) selections based on fruit quality, total anthocyanins, and antioxidant capacity. *Int. J. Food Prop.* **2011**, *14*, 471–480. [CrossRef]
- 20. Arivalagan, M.; Karunakaran, G.; Roy, T.K.; Dinsha, M.; Sindhu, B.C.; Shilpashree, V.M.; Satisha, G.C.; Shivashankara, K.S. Biochemical and nutritional characterization of dragon fruit (*Hylocereus species*). *Food Chem.* **2021**, 353, 129426. [CrossRef]
- 21. Sharma, O.P.; Bhat, T.K. Antioxidant activity and total phenols content of different varieties of Indian blackberry. *Food Chem.* **2009**, *113*, 1282–1289.
- 22. Sadasivam, S.; Manickam, A. Biochemical Methods, 3rd ed.; New Age International (P) Limited: New Delhi, India, 2007.
- 23. Matić, P.; Sabljić, M.; Jakobek, L. Validation of spectrophotometric methods for the determination of total polyphenol and total flavonoid content. *J. AOAC Intl.* **2017**, *100*, 1795–1803. [CrossRef] [PubMed]
- 24. 24. ASAE 368.2 Mar. 95; ASAE Standards. Compression Test of Food Materials of Convex Shape. American Society of Agricultural Engineers: St. Joseph, MI, USA, 1998; pp. 554–559.
- 25. Gopinath, P.P.; Parsad, R.; Joseph, B.; Adarsh, V.S. GrapesAgri1: Collection of shiny apps for data analysis in agriculture. *J. Open Source Softw.* **2021**, *6*, 3437. [CrossRef]
- 26. Jamaludin, N.A.; Ding, P.; Hamid, A.A. Physico-Chemical and structural changes of red-Fleshed dragon fruit (*Hylocereus polyrhizus*) during fruit development. *J. Sci. Food Agric.* **2011**, *91*, 278–285. [CrossRef] [PubMed]
- 27. Patel, R.K.; Singh, A.; Prakash, J.; Amit, N.; Deka, B.C. Physico-biochemical changes during fruit growth, development and maturity in passion fruit genotypes. *Indian J. Hortic.* **2014**, *71*, 486–493.
- 28. Chitarra, M.I.F.; Chitarra, A.B. Post-Harvesting of Fruits and Vegetables: Physiology and Handling, 2nd ed.; FAEPE: Lavras, Brazil, 2005; p. 785.
- 29. Tarte, I.; Singh, A.; Dar, A.H.; Sharma, A.; Altaf, A.; Sharma, P. Unfolding the potential of dragon fruit (*Hylocereus* spp.) for value addition: A review. *eFood* **2023**, *4*, 76. [CrossRef]

- 30. Lata, D.; Narayana, C.; Karunakaran, G.; Rao, S.D.V.; Sane, A. Maturity determination of red and white pulp dragon fruit. *J. Hort. Sci.* **2022**, *17*, 157–165. [CrossRef]
- 31. Ortiz, C.E.O.; Takahashi, L.S.A. Pitaya (*Hylocereus* spp.): Postharvest biology and technology of fruit. *Fruit Veg. Phytochem.* **2015**, 2, 1123–1138.
- Zitha, E.Z.M.; Magalhaes, D.S.; Lago, R.C.; Carvalho, E.E.N.; Pasqual, M.; Eduardo Val' erio de, B.V.B. Changes in the bioactive compounds and antioxidant activity in red-fleshed dragon fruit during its development. *Sci. Hortic.* 2022, 291, 110611. [CrossRef]
- 33. Junior, I.M.R.; Magalhaes, D.S.; Rodrigues, F.A.; Pasqual, M.; Pio, L.A.S. Fruit quality and harvest point determination in white-fleshed dragon fruit. *Res. Soc. Dev.* **2021**, *10*, 11810716287. [CrossRef]
- 34. Weiss, J.; Nerd, A.; Mizrahi, Y. Flowering behaviour and pollination requirements in climbing cacti with fruit crop potential. *Hort. Sci.* **1994**, *29*, 1487–1492.
- 35. Huang, M.; Zhao, J. Recent advances in postharvest storage and preservation technology of pitaya (dragon fruit). *J. Hortic. Sci. Biot.* **2023**, *99*, 115–129. [CrossRef]
- 36. Van To, L.; Ngu, N.; Duc, N.D.; Huong, H.T.T. Dragon fruit quality and storage life: Effect of harvesting time, use of plant growth regulators and modified atmosphere packaging. *Acta Hortic.* **2002**, *575*, 611–621. [CrossRef]
- Centurion Yah, A.R.; Solis Pereira, S.; Saucedo Veloz, C.; Baez Sanudo, R.; Sauri Duch, E. Sensorial, physical and chemical changes of pitahaya fruits (*Hylocereus undatus*) during development. J. Hort. Sci. 2008, 31, 1–5.
- 38. Le Bellec, F.; Vaillant, F.; Imbert, E. Pitahaya (*Hylocereus* spp.): A new fruit crop, a market with a future. *Fruits* **2006**, *61*, 237–250. [CrossRef]
- Kahkonen, M.P.; Hopia, A.I.; Heinonen, M. Berry phenolics and their antioxidant activity. J. Agric. Food Chem. 2001, 49, 4076–4082. [CrossRef]
- 40. Wongmetha, C.; Ke, L.S.; Liang, R.G.; Chang, C.C. Fruit firmness, cell wall composition and fruit quality of papaya during postharvest ripening. *Int. J. Agric. Biol.* **2015**, *17*, 351–356.
- Wanichang, J.; Jarimopas, B. Firmness and light reflectance properties of dragon fruits. In Proceedings of the Ninth National Conference of Thai Society of Agricultural Engineering on Technology for Sustainable Agriculture and Agroindustry, Chiangmai, Thailand, 31 January–1 February 2008.
- 42. Su, Q.; Li, X.; Wang, L.; Wang, B.; Feng, Y.; Yang, H.; Zhao, Z. Variation in cell wall metabolism and flesh firmness of four apple cultivars during fruit development. *Foods* **2022**, *11*, 3518. [CrossRef]
- 43. Ersan, K.; Yalcin, C.; Salih, A. Some physical fruit properties of cactus pear (Opuntia spp.) that grow wild in the eastern Mediterranean region of Turkey. *J. Prof. Assoc. Cactus Dev.* **2004**, *1*, 1–8.

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