

A Review of the Morphological Structure and Photosynthetic Metabolic Characteristics of Dragon Fruit (*Hylocereus* spp.)

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Abstract Dragon fruit (*Hylocereus* spp.) is widely cultivated in tropical and subtropical regions due to its unique appearance, rich nutritional value, and economic benefits. This study systematically analyzes the morphological structure and photosynthetic metabolic characteristics of dragon fruit, including its triangular stem segments, vibrant peel and pulp colors, and the adaptation mechanisms of its fleshy stem to arid environments. The research found that dragon fruit utilizes Crassulacean Acid Metabolism (CAM) photosynthesis, which reduces water loss by fixing carbon dioxide at night, demonstrating high drought resistance. Significant genetic variation among different species in traits such as fruit weight, carotenoid content, and antioxidant potential provides a theoretical basis for species identification and the selection of superior cultivars. The study also explores the growth cycle and physiological characteristics of dragon fruit, including flowering physiology, fruit development, and maturation processes. High temperatures and drought conditions significantly affect the growth and yield of dragon fruit, and the regulation of related genes, such as the expression of heat shock proteins, enhances its adaptability to environmental stress. Additionally, the economic value of dragon fruit cultivation is further enhanced by its potential in the development of health foods and nutritional supplements. This study provides a scientific basis for optimizing dragon fruit cultivation management, improving yield and quality, and offers research directions for further investigation into its disease resistance genes and the impact of climate change on dragon fruit production.

Keywords Dragon fruit (*Hylocereus* spp.); Morphological structure; Photosynthetic metabolism; Crassulacean Acid Metabolism (CAM); Genetic variation; Micropropagation

1 Introduction

Dragon fruit, belonging to the family of Cactaceae, is a tropical fruit that has gained significant popularity due to its unique appearance, nutritional benefits, and economic value. The fruit is rich in essential nutrients such as vitamins, minerals, complex carbohydrates, dietary fibers, and antioxidants, making it a valuable addition to the diet (Abirami et al., 2021). Dragon fruit is primarily cultivated in tropical and subtropical regions, with notable production in countries such as Vietnam, China, and Brazil (Wonglom et al., 2023; Zhao and Huang et al., 2023).

The morphological structure of dragon fruit includes distinctive features such as its vibrant peel and pulp colors, the presence of spines, and the unique shape of its cladodes. These characteristics not only contribute to its aesthetic appeal but also play a role in its identification and classification (Abirami et al., 2021; Xu et al., 2024). The photosynthetic metabolism of dragon fruit is adapted to its arid growing conditions, with specialized mechanisms that enhance its ability to thrive in such environments. Studies have shown significant genetic variation among different species of *Hylocereus*, particularly in traits related to fruit and pulp weight, carotenoid content, and antioxidant potential (Abirami et al., 2021).

Dragon fruit holds substantial economic value due to its high demand in both local and international markets. It is not only consumed fresh but also used in various processed forms such as juices, jams, and nutraceutical products. The fruit's high antioxidant content, particularly in its peel, makes it a potential candidate for the development of health supplements aimed at addressing vitamin deficiencies (Abirami et al., 2021). Additionally, the cultivation of dragon fruit provides economic opportunities for farmers in tropical regions, contributing to the agricultural economy (Zhao and Huang et al., 2023).

This study provides a comprehensive review of the research on the morphological structure and photosynthetic metabolic characteristics of dragon fruit (*Hylocereus* spp.). By analyzing its genetic variation, biochemical properties, and adaptive mechanisms, the study offers an in-depth exploration of the growth and development patterns of dragon fruit. Furthermore, it highlights the economic value of dragon fruit and its potential applications in the nutrition and health industry. Through this research, we aim to identify key traits that can be utilized to improve the cultivation and utilization of dragon fruit, thereby promoting the advancement of agricultural production and economic development in tropical regions.

2 Morphological Characteristics and Structural Adaptations of *Hylocereus* spp.

2.1 Climbing habit and stem morphology

Dragon fruit (*Hylocereus* spp.) is a climbing cactus species characterized by its sprawling, three-sided (triangular) stems, which are typically green and segmented. The climbing habit of the plant is facilitated by aerial roots that emerge from the stem nodes, allowing it to attach to support structures such as trees, rocks, or trellises (Subandi et al., 2018; Sharma et al., 2023). The stems of dragon fruit, known as cladodes, serve as the primary photosynthetic organs and are also the main sites for water storage, which is crucial for the plant's survival in its native arid environments (Yadav et al., 2024).

The stems of dragon fruit have ribbed structures, with each segment displaying prominent margins and areoles, typically bearing 3 to 5 spines per areole, a distinctive feature of the plant (Sharma et al., 2023). The length of the spines ranges from 1 to 4 millimeters, and the ribbed margins of the stem segments can be either raised or depressed. This structural configuration aids the dragon fruit plant in climbing and adhering to support structures (Abirami et al., 2021). The vertical growth habit of the plant not only allows it to achieve optimal light exposure but also reduces competition for ground resources. This growth pattern is particularly advantageous in dense forest canopies or cultivated settings, effectively utilizing vertical space.

2.2 Adaptations of the fleshy stem

The fleshy stem of the dragon fruit is an evolutionary adaptation with two main functions: water storage and photosynthesis. The succulent nature of the stem enables it to store a significant amount of water, providing a reserve during periods of drought (Wakchaure et al., 2021). This adaptation is particularly crucial for the survival of dragon fruit in its native arid environments, where water availability is unpredictable. Additionally, the stem serves as the primary photosynthetic organ for the dragon fruit, as *Hylocereus* spp. lacks significant leaf structures. This plant utilizes a specialized form of photosynthesis known as Crassulacean Acid Metabolism (CAM), which allows it to open its stomata at night to reduce water loss while using the stored carbon dioxide for photosynthesis during the day (Sahu et al., 2022).

The thick waxy cuticle on the stem surface further reduces water evaporation by forming a barrier that prevents dehydration, thereby protecting the plant (Abirami et al., 2021; Salunkhe et al., 2022a; 2022b). While the stem carries out photosynthesis and water storage, its ribbed structure also enhances light absorption and facilitates gas exchange. This morphological feature allows the dragon fruit to maintain photosynthetic activity even under low water conditions, enhancing its resilience to varying climatic conditions.

2.3 Root system adaptations

The root system of dragon fruit exhibits several adaptations that enhance its ecological significance. Dragon fruit plants possess both aerial and terrestrial roots. The aerial roots, which emerge from the stems, help the plant climb and anchor itself to various structures (Xu et al., 2024). These roots can absorb moisture and nutrients from the air, which is particularly beneficial in humid environments. The terrestrial roots, on the other hand, penetrate the soil and provide stability and access to water and nutrients. This dual root system allows dragon fruit to exploit multiple ecological niches, enhancing its adaptability and resilience in diverse growing conditions (Abirami et al., 2021; Wang et al., 2021; Parameswari et al., 2022).

By understanding these morphological characteristics and structural adaptations, researchers and cultivators can better appreciate the resilience and versatility of dragon fruit, which contributes to its increasing popularity and cultivation in various regions around the world.

3 Photosynthetic Metabolic Characteristics of Dragon Fruit (*Hylocereus* spp.)

3.1 Overview of CAM photosynthesis in dragon fruit

Dragon fruit (*Hylocereus* spp.) utilizes Crassulacean Acid Metabolism (CAM) photosynthesis, a specialized form of photosynthesis adapted to arid conditions (Xu et al., 2024). CAM plants, including dragon fruit, fix CO₂ at night, which is a reversal of the typical daytime CO₂ fixation seen in C3 and C4 plants. This nocturnal CO₂ fixation helps minimize water loss, making CAM photosynthesis particularly advantageous in drought-prone environments (Yamori et al., 2014). The CAM pathway in dragon fruit involves a complex regulatory network of genes, including those associated with the circadian clock, which orchestrates the timing of metabolic processes to optimize photosynthetic efficiency (Ma et al., 2021).

3.2 Carbon fixation patterns

In dragon fruit, the CAM pathway is characterized by distinct day and night phases of carbon fixation. At night, CO₂ is fixed into organic acids, primarily malate, which is stored in vacuoles. During the day, the stored malate is decarboxylated to release CO₂ for the Calvin cycle, enabling photosynthesis to proceed while stomata remain closed to conserve water (Wang et al., 2019). This diurnal rhythm is regulated by a suite of genes, including MALATE DEHYDROGENASE (MDH), MALIC ENZYMES (ME), and PYRUVATE PHOSPHATE DIKINASE (PPDK), which exhibit peak expression levels at specific times of the day and night, ensuring efficient carbon fixation and utilization (Ma et al., 2021).

3.3 Adaptation strategies under drought and high light conditions

Dragon fruit (*Hylocereus* spp.) has evolved several adaptation strategies to thrive under drought and high light conditions. One of the most significant adaptations is the utilization of the Crassulacean Acid Metabolism (CAM) photosynthetic pathway, which minimizes water loss by opening stomata during the cooler night hours, thereby reducing transpiration (Wang et al., 2019; Lee et al., 2023). This pathway allows the plant to maintain photosynthetic activity even under extreme environmental stress.

Additionally, dragon fruit exhibits morphological traits such as thick, waxy cladodes that reduce water loss and reflect excess light. The plant's ability to modulate the expression of CAM-related genes in response to environmental stress further enhances its resilience. For instance, genes involved in the CAM pathway show rhythmic expression patterns that are finely tuned to environmental cues, optimizing water use efficiency and photosynthetic performance under varying conditions (Abirami et al., 2021; Ma et al., 2021).

3.4 Comparison with photosynthesis in other fruit trees

Compared to other fruit trees that primarily utilize C3 or C4 photosynthesis, dragon fruit's CAM pathway offers distinct advantages in arid environments. C3 plants, which include many temperate fruit trees, fix CO₂ directly through the Calvin cycle during the day, leading to higher water loss through open stomata. C4 plants, such as maize, have a more efficient CO₂ fixation mechanism that reduces photorespiration but still primarily operates during the day (Yamori et al., 2014).

In contrast, the nocturnal CO₂ fixation in CAM plants like dragon fruit significantly reduces water loss, making them better suited to hot, dry climates. This unique adaptation not only supports the survival of dragon fruit in challenging environments but also contributes to its ability to produce high yields of nutrient-rich fruit under conditions that would be detrimental to many other fruit trees (Abirami et al., 2021; Ma et al., 2021).

4 Growth Cycle and Developmental Physiology

4.1 Growth stages

The seedling stage of dragon fruit (*Hylocereus* spp.) begins with germination, where seeds sprout and develop into young plants. This stage is crucial for establishing a strong root system and initial shoot growth. The early

development phase involves the formation of cladodes, which are modified stems that will later support the plant's growth and fruit production (Chu and Chang, 2020). During the vegetative growth stage, dragon fruit plants exhibit significant branching and canopy formation. Cladodes grow and multiply, forming a dense canopy that maximizes photosynthetic efficiency. Morphological traits such as the number of spines, length of areoles, and the waxiness of cladodes are important for identifying different *Hylocereus* species (Figure 1) (Abirami et al., 2021). This stage is characterized by rapid growth and the establishment of a robust plant structure.



Figure 1 An illustration of important traits of three different *Hylocereus* species of dragon fruit. Cladode characters: (A) length of segments (cm), (B) number of spines and (C) margin ribs of cladode; Flower characters: (D) flower bud shape and (E) shape of apex; fruit characters: (F) fruit length (cm) and (G) position towards the peel (Adopted from Abirami et al., 2021)

Image caption: The figure provides a detailed illustration of the differences in key morphological traits, including cladode segments, flower buds, and fruits, among three dragon fruit (*Hylocereus* spp.) species. The results indicate significant interspecies differences in these traits. For example, the cladode margin of *H. megalanthus* (DGF3) is concave, while it is convex in the other two species. The fruit shape and flower apex morphology also show distinct variations. These differences highlight the importance of morphological traits in distinguishing dragon fruit species and demonstrate their application value in species identification (Adapted from Abirami et al., 2021)

The reproductive phase of dragon fruit includes the flowering and fruiting periods. Flowering is induced by specific environmental signals, and the development of flowers leads to fruit production (Mallik et al., 2018). For instance, a study on red-fleshed pitaya ‘Da Hong’ (*Hylocereus polyrhizus*) found that high-temperature treatment (40/30 °C) significantly suppressed fruit development, resulting in a substantial decrease in fruit set, seed weight, and fruit weight (Chu and Chang, 2020). The reproductive success of dragon fruit is also influenced by various factors, including pollination mechanisms and the plant's genetic characteristics (Abirami et al., 2021). This phase is crucial for the yield and quality of the fruit.

4.2 Flowering physiology

Floral induction in dragon fruit is triggered by environmental factors such as temperature and photoperiod. The development of flowers involves a series of physiological changes that prepare the plant for reproduction. The timing and intensity of flowering can vary among different *Hylocereus* species, influenced by their genetic makeup and environmental conditions (Mallik et al., 2018). Pollination in dragon fruit is primarily achieved through nocturnal pollinators such as bats and moths. Successful pollination is essential for fruit set and development. The reproductive success of dragon fruit can be affected by the availability of pollinators and the compatibility of pollen and stigma. Genetic variations among *Hylocereus* species can also influence pollination efficiency and fruit production (Ador et al., 2024).

Several factors can affect the flowering time and intensity of dragon fruit, including temperature, light, and water availability. Stress conditions such as drought or nutrient deficiency can delay flowering or reduce the number of flowers produced. Understanding these factors is crucial for optimizing flowering and maximizing fruit yield (Abirami et al., 2021).

4.3 Fruit development and maturation

Fruit development in dragon fruit involves two main stages: cell division and cell enlargement. During the initial stage, rapid cell division occurs, leading to the formation of the fruit structure. This is followed by cell enlargement, where the fruit increases in size and accumulates nutrients. Morphological traits such as fruit and pulp weight, as well as the color of the peel and pulp, are important indicators of fruit development (Trong et al., 2022). Ripening of dragon fruit involves several physiological changes, including the accumulation of sugars, acids, and pigments. These changes contribute to the fruit's flavor, color, and nutritional content. The antioxidant potential of dragon fruit is higher in the peel than in the pulp, with significant variations in phenol and flavonoid content among different *Hylocereus* species (Abirami et al., 2021).

Fruit quality and yield in dragon fruit are influenced by genetic, environmental, and management factors. Xu et al. (2024) found that spraying 100 ppm gibberellin, 10 ppm forchlorfenuron, and 1 000 ppm slow-release nitrogen fertilizer during the first fruit expansion period can extend the fruit-bearing period to 40 days and increase the soluble solids content to 21.5% (Table 1). Effective management practices, including pest and disease control, are essential for optimizing fruit yield and quality (Abirami et al., 2021; Wonglom et al., 2023; Zhao and Huang, 2023). By understanding the growth cycle and developmental physiology of dragon fruit, researchers and growers can implement strategies to enhance fruit production and quality, ensuring the sustainability and profitability of this important tropical fruit crop.

5 Environmental Response Mechanisms of *Hylocereus* spp.

5.1 Response to light intensity

Hylocereus spp. exhibit a remarkable ability to adapt to varying light conditions, which is crucial for their survival and productivity. As a member of the Cactaceae family, dragon fruit plants are well-suited to thrive in high-light environments (Abirami et al., 2021; Kakade et al., 2022). Their stems, which serve as the primary photosynthetic organ, contain a thick waxy cuticle and sunken stomata, which help reduce water loss under intense light conditions.

However, excessive light exposure can lead to photoinhibition and chlorophyll degradation, impacting photosynthetic efficiency. To counteract this, *Hylocereus* spp. activate photoprotective mechanisms such as the

xanthophyll cycle, which dissipates excess light energy as heat, thus preventing damage to the photosynthetic apparatus (Espley and Jaakola, 2023). Additionally, the orientation of the cladodes (modified stems) can be adjusted to minimize direct sunlight exposure, further enhancing light management.

Table 1 Evaluation of appearance and soluble solids content after tree treatment (Adopted from Xu et al., 2024)

| Group | Indicators | Days after flowering | | | | | |
|-----------------|---------------------|----------------------|--------|----------|--------------|--------------|--------------|
| | | 20 d | 25 d | 30 d | 35 d | 40 d | 45 d |
| Treatment Group | Weight (g) | 370 | 424 | 487 | 510 | 515 | 517 |
| | Sweetness (% Brix) | 11 | 15 | 17 | 21 | 20.5 | 20 |
| | Scale integrity | Intact | Intact | Intact | Intact | Intact | Intact |
| | Fruit surface color | Green | Yellow | Yellow | Yellow-green | Green | Green |
| Control group | Weight (g) | 359 | 410 | 458 | 472 | 480 | 473 |
| | Sweetness (% Brix) | 11 | 15 | 17 | 18 | 17 | 15 |
| | Scale integrity | Intact | Intact | Dry tips | Withered | Withered | Cracked |
| | Fruit surface color | Green | Yellow | Yellow | Yellow-green | Yellow-green | Yellow-green |

5.2 Temperature tolerance and adaptation

Temperature is another critical factor influencing the growth and development of *Hylocereus* spp. These plants are highly adapted to withstand high temperatures, typical of arid and semi-arid environments, where they often thrive. Optimal growth occurs between 18 °C and 35 °C, but they can tolerate temperatures as high as 40 °C (Chu and Chang, 2020). In response to heat stress, *Hylocereus* spp. employ several physiological mechanisms, including the upregulation of heat shock proteins (HSPs) and the stabilization of cell membranes (de Oliveira et al., 2021). These adaptations help maintain cellular homeostasis and prevent thermal damage to enzymes involved in metabolic processes. Conversely, *Hylocereus* spp. are sensitive to low temperatures, particularly frost, which can cause tissue damage and necrosis. To mitigate the effects of cold stress, these plants may accumulate osmolytes such as proline and soluble sugars, which act as cryoprotectants by stabilizing cellular structures and maintaining osmotic balance.

5.3 Response to water availability

The ability of *Hylocereus* spp. to adapt to water scarcity is one of its most distinctive features, enabling it to thrive in environments with irregular rainfall. As CAM (Crassulacean Acid Metabolism) plants, dragon fruit species exhibit a unique water-conserving strategy by opening their stomata at night to minimize water loss during photosynthesis (Wang et al., 2019; Jalgaonkar et al., 2022). During periods of drought, *Hylocereus* spp. can shift their CAM activity towards a more conservative water-use mode, characterized by reduced stomatal opening and increased water-use efficiency (Wang et al., 2019). The fleshy stems serve as water reservoirs, storing large quantities of water that sustain the plant during prolonged dry spells.

Additionally, the root system of *Hylocereus* spp. is adapted to maximize water uptake from the soil, with a high density of fine roots that can rapidly absorb moisture from transient rainfalls (Wakchaure et al., 2023). These adaptations collectively enhance the plant's drought tolerance, making *Hylocereus* spp. a resilient crop for cultivation in arid and semi-arid regions.

6 Case Studies

6.1 Liquid culture system enhances dragon fruit micropropagation efficiency

Dragon fruit (*Hylocereus* spp.) exhibits remarkable adaptability in arid and semi-arid environments, which is crucial for cultivation in water-deficient areas (Wakchaure et al., 2023). However, conventional propagation methods are limited by low multiplication rates and high production costs. Some studies have explored methods to improve large-scale micropropagation of dragon fruit using automated liquid culture systems (Dewir et al., 2023; Lee and Chang, 2024). For example, a study on the large-scale micropropagation of red-fleshed dragon fruit (*Hylocereus polyrhizus*) using an automated liquid culture system and arbuscular mycorrhizal fungi (AMF) demonstrated that the proliferation of axillary buds in a continuous immersion air-lift bioreactor system

significantly outperforms gelled culture, increasing the number of axillary buds by six times (Dewir et al., 2023). The proliferation rate of axillary buds in the bioreactor system reached 45.9 buds per explant, compared to only 6.7 buds per explant in gelled culture (Figure 2). Additionally, inoculation with AMF (*Gigaspora margarita* and *Gigaspora albida*) significantly promoted the growth of micropropagated plantlets during acclimatization, improving leaf pigment content and biomass accumulation.

AMF enhances water and nutrient absorption through symbiosis with the root system of dragon fruit, boosting the plant's photosynthetic capacity and stress resistance (Dewir et al., 2023). These results indicate that combining liquid culture and AMF technology can achieve large-scale commercial micropropagation of dragon fruit while ensuring seedling quality, presenting broad application prospects. This study provides an efficient and feasible technological approach for the industrial-scale propagation of dragon fruit.

6.2 Performance in tropical regions: growth and productivity

In tropical regions, dragon fruit exhibits vigorous growth and high yield characteristics (Abirami et al., 2021; Sahu et al., 2023). In a study conducted in the Andaman and Nicobar Islands of India, three dragon fruit species were identified based on morphological, biochemical, and molecular markers. Abirami et al. (2021) found significant genetic variation among different dragon fruit species, especially in fruit characteristics such as peel and pulp color, which is crucial for distinguishing different species. Moreover, molecular characterization using 14 ISSR primers revealed high genetic diversity among genotypes, allowing differentiation of species based on geographic origin and pulp color.

Regarding biochemical traits, the study indicated that phenolic and flavonoid content was higher in the peel than in the pulp, suggesting a greater antioxidant potential in the peel. Significant differences were observed in total carotenoid and β -carotene content among the different genotypes, with DGF4 and DGF2 showing higher levels, indicating their high nutritional and industrial value (Abirami et al., 2021). Cluster analysis using ISSR markers grouped these dragon fruit genotypes into two clusters based on geographical location and pulp color.

Overall, the analysis shows that these traits can effectively distinguish different dragon fruit species and have potential value for developing nutraceutical products, especially for addressing vitamin A deficiency in tropical populations. Future research can further utilize these genotypes to develop functional foods and nutritional supplements.



Figure 2 Multiplication and growth of *H. polyrhizus* in gelled culture versus bioreactor culture after 8 weeks (Adopted from Dewir et al., 2023)

Image caption: (a) shows the initial stage of the air-lift bioreactor system, while (b) and (c) display the growth of axillary buds in the liquid culture at 4 and 8 weeks, respectively. (d) illustrates the growth of axillary buds in the gelled culture after 8 weeks. In (e), the bioreactor culture (42.8 and 45.9 axillary buds) significantly outperformed the gelled culture (6.7 axillary buds) in terms of bud number, fresh weight, and length. This indicates that the liquid culture system is more suitable for the proliferation of dragon fruit axillary buds than gelled culture, demonstrating its potential to effectively increase yield and quality in large-scale micropropagation (Adapted from Dewir et al., 2023)

6.3 Study on genome rearrangement and metabolic adaptation of dragon fruit

Dragon fruit (*Hylocereus* spp.) is a tropical fruit with high economic value, widely recognized for its rich nutritional content and unique antioxidant properties (Hossain et al., 2021). However, the understanding of its genome structure and evolutionary history remains limited. Zheng et al. (2021) have constructed the first chromosome-level genome assembly of dragon fruit and revealed a whole-genome duplication (WGD) event. The study found that the common ancestor of dragon fruit and other cacti experienced a WGD event, followed by significant genome rearrangements. These changes may have contributed to the adaptation of cacti to arid environments. Genes related to antioxidant defense, amino acid metabolism, and photosynthesis are enriched in dragon fruit-specific OGCs. The expansion and expression regulation of these genes contribute to enhancing the stress resistance and nutritional value of dragon fruit (Figure 3). Moreover, key genes in the betacyanin biosynthesis pathway are co-localized in a 12 Mb region on one chromosome in dragon fruit. This gene co-localization may enhance the efficiency of betacyanin biosynthesis, thereby contributing to the high antioxidant capacity of dragon fruit (Zheng et al., 2021). This research not only reveals the unique evolutionary and metabolic mechanisms of dragon fruit but also provides valuable resources for future breeding and functional gene studies based on genomic information.

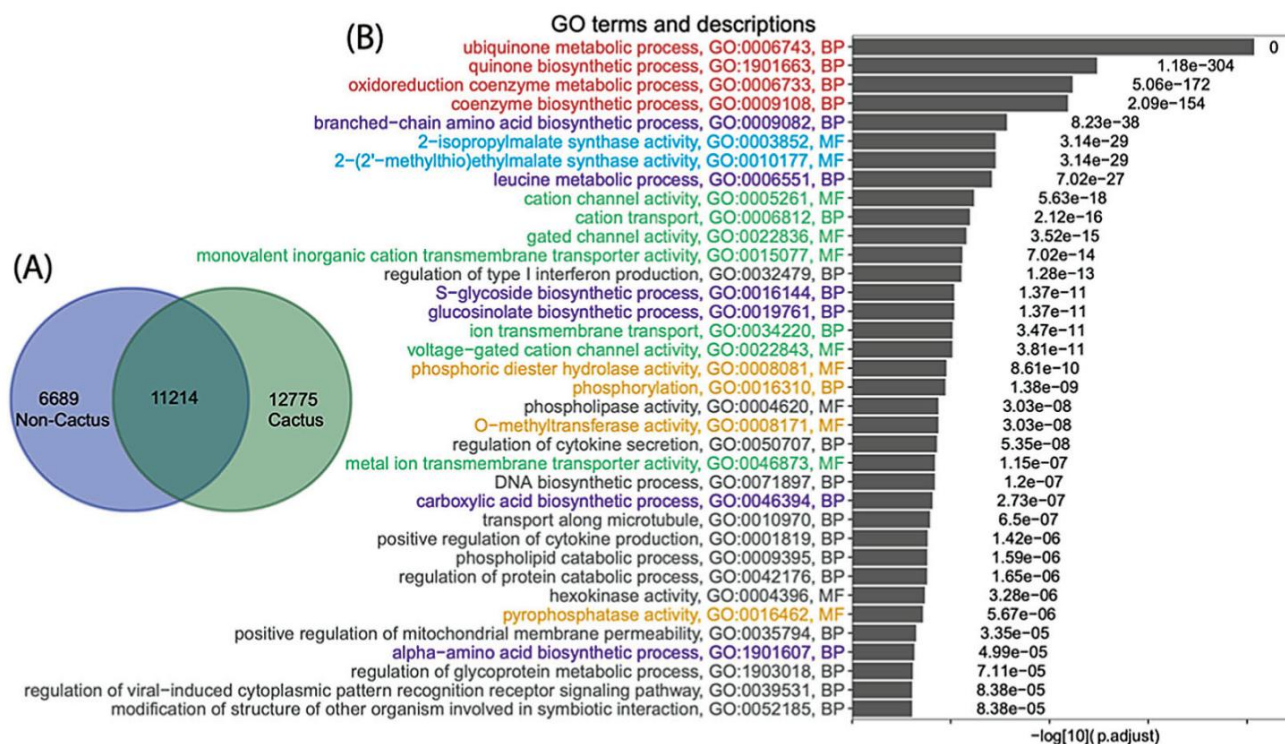


Figure 3 GO enrichment analysis of orthologous gene clusters (OGCs) in cactus and noncactus plants. (A) 30,457 OGCs are clustered into 12 755 cactus-specific OGCs, 6689 noncactus-specific OGCs, and 11 214 shared OGCs. (B) GO enrichment analysis was conducted with 12 775 cactus-specific OGCs as foreground, and 11 214 shared OGCs as background. The x axis shows the log10 of the adjusted P values, and the y axis shows the GO terms (only molecular function (MF) and biological process (BP) are shown) with adjusted P value < 0.01. Groups of GO terms are colored in green (group I), red (group II), purple (group III), blue (group IV), and orange (group V) (Adopted from Zheng et al., 2021)

Image caption: Figure 3A categorizes 30,457 OGCs into three types: cactus-specific, non-cactus-specific, and shared OGCs. Figure 3B shows that significantly enriched GO functions in cactus-specific OGCs include ion channels (related to osmotic stress and stomatal regulation), antioxidant defense, amino acid and biosynthetic metabolism, CAM photosynthesis, and phosphorylation and methylation metabolism. This figure indicates that cactus plants have enhanced their drought resistance and environmental adaptability through the expansion of these functional genes during evolution, confirming the crucial role of these genes in drought and high-temperature conditions (Adapted from Zheng et al., 2021)

In summary, dragon fruit (*Hylocereus* spp.) exhibits remarkable morphological and photosynthetic adaptations, allowing it to thrive in various environments ranging from arid and semi-arid regions to tropical climates and controlled agricultural systems (Abirami et al., 2021; Dewir et al., 2023; Wakchaure et al., 2023). These adaptations are supported by genetic traits that enhance drought resistance and antioxidant potential, making dragon fruit a versatile and economically valuable crop.

7 Implications for Cultivation and Management Practices of Dragon Fruit (*Hylocereus* spp.)

7.1 Optimization of light and water management for improved growth

Effective light and water management are crucial for the optimal growth of dragon fruit (*Hylocereus* spp.). Dragon fruit plants are known for their ability to survive under less water and poor-quality soils, which makes them suitable for cultivation in arid and semi-arid regions (Salunkhe et al., 2022b). However, intermittent and untimely rains can exacerbate disease conditions such as anthracnose, which affects the overall health and yield of the plants (Salunkhe et al., 2022b). Therefore, implementing controlled irrigation systems that provide consistent moisture levels without waterlogging can help mitigate disease risks and promote healthy growth. Additionally, ensuring adequate light exposure is essential, as dragon fruit plants thrive in well-lit environments (Zhang et al., 2022). Utilizing shade nets or adjusting plant spacing can optimize light penetration and reduce the incidence of diseases caused by excessive moisture.

7.2 Soil and nutrient management for maximizing yield and quality

Soil and nutrient management play a pivotal role in maximizing the yield and quality of dragon fruit. The use of organic fertilizers has been identified as a beneficial practice, although its application is currently minimal among producers (Pérez et al., 2023). Enhancing soil fertility through the incorporation of organic matter and balanced fertilization can improve plant health and fruit quality. Regular soil testing and tailored nutrient management plans can ensure that the plants receive the necessary macro and micronutrients. Additionally, addressing soil-borne diseases through proper sanitation and crop rotation practices can further enhance yield and quality. For instance, the management of stem canker caused by *Neoscytalidium dimidiatum* requires careful monitoring and timely intervention to prevent significant yield losses (Salunkhe et al., 2022a).

7.3 Controlled environment adaptations

Adapting controlled environment agriculture (CEA) techniques such as greenhouse and vertical farming can offer significant advantages for dragon fruit cultivation. These methods provide a controlled environment that can mitigate the impact of adverse weather conditions and reduce the incidence of diseases (Neo et al., 2022). Greenhouses can protect plants from excessive rainfall, which has been linked to the spread of anthracnose and other fungal diseases (Salunkhe et al., 2022a; 2022b). Vertical farming, on the other hand, can optimize space utilization and enhance light exposure, leading to improved growth and yield. Implementing these advanced cultivation techniques can also facilitate better pest and disease management, ensuring a consistent and high-quality production of dragon fruit. By integrating these optimized cultivation and management practices, dragon fruit producers can enhance the overall productivity and sustainability of their operations, leading to improved economic outcomes and market potential.

8 Concluding Remarks

The morphological and photosynthetic characteristics of dragon fruit (*Hylocereus* spp.) have been extensively studied, revealing significant genetic variation and biochemical diversity among different species. Morphological traits such as the number of spines, length of areoles, and the color of the peel and pulp are key identifiers for distinguishing between species. Additionally, the biochemical analysis has shown that the peels of dragon fruit have higher phenol and flavonoid content compared to the pulp, indicating a higher antioxidant potential. The presence of high carotenoid and xanthophyll content in certain genotypes suggests their potential for industrial applications in nutraceutical products. Furthermore, the identification of new fungal pathogens affecting dragon fruit, such as *Neoscytalidium hylocereum* and *Fusarium* spp., highlights the importance of understanding the plant's disease resistance mechanisms.

Despite the progress made in understanding the morphological and biochemical traits of dragon fruit, several research gaps remain. Firstly, there is a need for more comprehensive studies on the photosynthetic efficiency and metabolic pathways of different *Hylocereus* species under varying environmental conditions. This could provide insights into optimizing growth and yield. Secondly, the genetic basis of disease resistance in dragon fruit is not well understood. Future research should focus on identifying resistance genes and developing disease-resistant cultivars, especially against newly identified pathogens like *Neoscytalidium hylocereum* and *Fusarium concentricum*. Additionally, the impact of climate change on the growth, yield, and disease susceptibility of dragon fruit warrants further investigation.

The findings from morphological and biochemical studies of dragon fruit have several practical applications. In agriculture and horticulture, the identification of key morphological traits can aid in the selection and breeding of superior cultivars with desirable characteristics such as higher antioxidant content and disease resistance. The high carotenoid and xanthophyll content in certain genotypes can be leveraged in the nutraceutical industry to develop products that address vitamin-A deficiency in tropical regions. Moreover, understanding the sensitivity of dragon fruit pathogens to various fungicides can guide effective disease management practices, ensuring sustainable production. Overall, these applications can enhance the economic value and health benefits of dragon fruit, promoting its cultivation and utilization on a larger scale.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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