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Genetic Regulation of Nocturnal Flowering in Pitaya Floral Morphology, Olfactory Cues, and Pollination Adaptation

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Abstract This study investigated the genetic regulation mechanism of night flowering in Pitaya (*Hylocereus* spp.). In the application of multi-omics technology, transcriptome and metabolome analysis were used to reveal the central role of sugar and hormone signaling in flower bud induction, as well as the potential role of epigenetic and miRNA in flowering regulation. The flower structure and aroma components showed a high degree of coordination with nocturnal pollinators, providing a new perspective for understanding the pollination adaptation of pitaya fruit. The integration of genetic and environmental factors plays a very important role in optimizing the flowering time and breeding strategy of Pitaya fruit, improving the yield and quality of Pitaya fruit, and providing theoretical basis for future research.

Keywords Pitaya; Nocturnal flowering; Genetic regulation; Multi-omics analysis; Pollination adaptation

1 Introduction

Pitaya (*Hylocereus spp.*), is becoming more and more popular. pitaya tastes good, looks attractive, and is good for health. People like pitaya because it is rich in healthy substances such as vitamins, antioxidants and fiber (Xiong et al., 2020; Wu et al., 2022). pitaya is also becoming more and more valuable financially and more and more people want to buy it. To produce more and better fruit. If you want to see pitaya outside the normal growing season, you need to understand how pitaya flowers grow and develop.

The flowering process is a critical stage in the growth of pitaya, which affects the yield and quality of pitaya. Affected by many factors such as genes and environment, the growth process of pitaya flower is very complicated. pitaya flowers exhibit a unique nocturnal flowering pattern, which is regulated by circadian rhythms and can attract specific pollinators (Prieto-Benitez et al., 2016; Ye et al., 2021; Shah et al., 2025). Genetic regulation of flowering, signaling pathways associated with sugar and hormone signaling, is critical for flower bud formation and subsequent flowering (Wu et al., 2022; Shah et al., 2025). Understanding these mechanisms to find ways to improve flowering timing and increase fruit yield, especially in the absence of natural pollinators (Muniz et al., 2019; Wang et al., 2023).

This study will investigate how pitaya regulates flowering at night. Understanding flower structure, smell, and how plants adapt to pollinators, understanding which genes and other factors influence these processes, and knowing this information can lead to better ways to grow pitaya and produce more fruit. This study puts forward suggestions on the problems existing in pitaya research and industrial development and the future research direction, and provides reference and basis for the production and scientific research of pitaya.

2 Floral Development in Pitaya

2.1 How floral organs develop

There are many different genes and plant hormones involved in the growth of pitaya flowers. Transcriptome analysis showed that the activity of many genes varied at different stages of peanut growth, mainly involved in hormone signaling, energy utilization, carbohydrate transport and gene expression. The hormones indole-3-acetic acid, abscisic acid and ethylene are important in the flowering process (Wu et al., 2022). Genes related to sugar production and motility are also very important and contribute to flower growth, suggesting that flower organ development in Pitaya is regulated by genetic mechanisms (Wu et al., 2022).

Some studies found important genes called *CONSTANS-LIKE* and *FLOWERING LOCUS T*. These genes help control when pitaya flowers. They work together with other genes like CDF and TCP. These genes act like switches that turn other genes on or off. They respond to things like how long the day is and plant hormones. Because of this, the way genes control flowering in pitaya is not simple (Xiong et al., 2020).

2.2 Flowering time of pitaya

Pitaya flowers open at night and close by early morning. This nocturnal habit matches well with the activities of pollinators that are active at night, like moths. This pattern helps ensure flowers are open when these pollinators visit (Ye et al., 2021). Environmental factors can affect when pitaya flowers bloom. For example, using extra lights during short winter days can encourage pitaya to bloom even out of its normal season (Xiong et al., 2020).

The *HuNIP6-1* gene helps control when flowers bloom. The researchers tested the gene in Arabidopsis thaliana, where overexpression of the gene promotes early flowering. *HuNIP6; 1* gene may also help control the flowering time of pitaya, and this gene can be used to change the flowering time of pitaya, and also help to plant more fruit and improve the yield (Ye et al., 2021).

2.3 Differences among pitaya varieties

Different kinds of pitaya flower in different ways. pitaya flowers can be larger or smaller, the opening time is also different, some early, some late. Researchers observed red pitaya and found that different genes play different roles in flower growth, so different pitaya types have different flower appearance and behavior (Wu et al., 2022).

Different species of pitaya have different pollination methods, and *Hylocereus undatus* can grow fruit on its own without the help of insects or animals. If you want red meat pitaya (*H. polyrhizus*), you need pollinators to grow larger fruit. Not all pitayas flower or bear fruit in the same way (Muniz et al., 2019). Because of the variety of Pitaya flowering traits, optimizing these traits can produce more fruits and better quality Pitaya varieties.

3 Genetic Control of Flowering Time of Pitaya Fruit

3.1 Regulation of genes related to circadian rhythm

Circadian rhythms work by integrating environmental signals with biological processes inside the plant, and it helps the plant decide the right time to bloom by matching internal signals with external conditions, such as light and dark. In *Arabidopsis thaliana*, this clock involves genes such as *TOC1*, *CCA1* and *LHY*, several genes that work together to turn each other on and off, controlling when flowering genes are activated. Let the flowers open at the best time and grow in an environment suitable for reproduction.

Through the interaction of multiple genes, such as *PRR* genes (such as *PRR9, PRR7* and *PRR5*) help promote the key photoperiodic regulator *CONSTANS* (*CO*) genes, regulate the level of *CO* expression, to control the timing of flowering. This is also one of the functions of circadian rhythm regulation, and also shows the importance of synchronizing flowering with environmental signals.

3.2 Genes that respond to day length

The length of day and night (called photoperiod) strongly affects when plants flower. A key gene that senses day length in pitaya fruit is called *CONSTANS* (*CO*). *CO* takes signals from the circadian clock and the amount of light and uses them to turn on another gene called *FLOWERING LOCUS T* (*FT*). *FT* then triggers the flowering process. Genes like *TOC1*, *CCA1*, and *LHY*, which are part of the circadian clock, also connect closely with the CO-FT pathway. Together, they make sure flowering happens at the right season.

The *EARLY FLOWERING 3* (*ELF3*) *and GIGANTEA* (*GI*), are also important. They help plants know how long the day and night are. These genes pass that information to the plant's internal clock, helping the plant decide exactly when to flower. This network of genes makes sure the timing of flowering matches the environment closely (Anwer et al., 2019).

3.3 RNA-seq reveals regulatory lineage

RNA sequencing (RNA-SEQ) technology can be used to reveal the molecular mechanism of flowering time regulation. pitaya usually blooms during a long day, and RNA-seq analysis has found that many differentially expressed genes (DEGs) are involved in energy metabolism and plant hormone signaling pathways, which can induce flowering in pitaya under the condition of light supplementation (Xiong et al., 2020). Key genes such as *CONSTANS-LIKE* and *FLOWERING LOCUS T* can be identified, which are involved in flowering regulation. From this phenomenon, it can be seen that there is a complex molecular network of photoperiodic change response in Pitaya fruit.

RNA-seq also found other important genes, such as *HuNIP6; 1* gene, a water channel protein gene, is also involved in the flowering process of pitaya fruit. HuNIP6 was overexpressed in *Arabidopsis Thaliana.* The *HuNIP6; 1* gene can inhibit the expression of flowering inhibitory factors, and then promote early flowering. *HuNIP6; 1* gene has a potential function in regulating flowering time (Ye et al., 2021). These findings provide a systematic perspective for understanding the genetic regulation of flowering time and provide potential targets for optimizing crop flowering traits by molecular means.

4 Hormonal Control of Flowering

4.1 The role of gibberellins (GA) in flower bud formation

Gibberellins (GA) play a key role in the transition from vegetative stage to reproductive stage of Pitaya fruit. During flower bud induction, the content of active gibberellin (such as GA3 and GA4) was significantly reduced, suggesting that gibberellin may slow or prevent the flowering of pitaya. This is consistent with the cognitive non-regression of flowering promotion in other plants (Shah et al., 2025), suggesting that hormonal regulation is complex and important in the flowering process of pitaya.

Gibberellin interacts with other hormones in the plant, interacts with a variety of transcription factors and flowering related genes to regulate the flowering process. Differentially expressed during flower bud induction. Gibberellin is a key gene involved in the regulation of flowering processes by affecting signaling pathways related to photoperiod and developmental age (Figure 1) (Shah et al., 2025). Understanding the role of gibberellin in the flowering of pitaya helps to understand how flowers form in other plants.

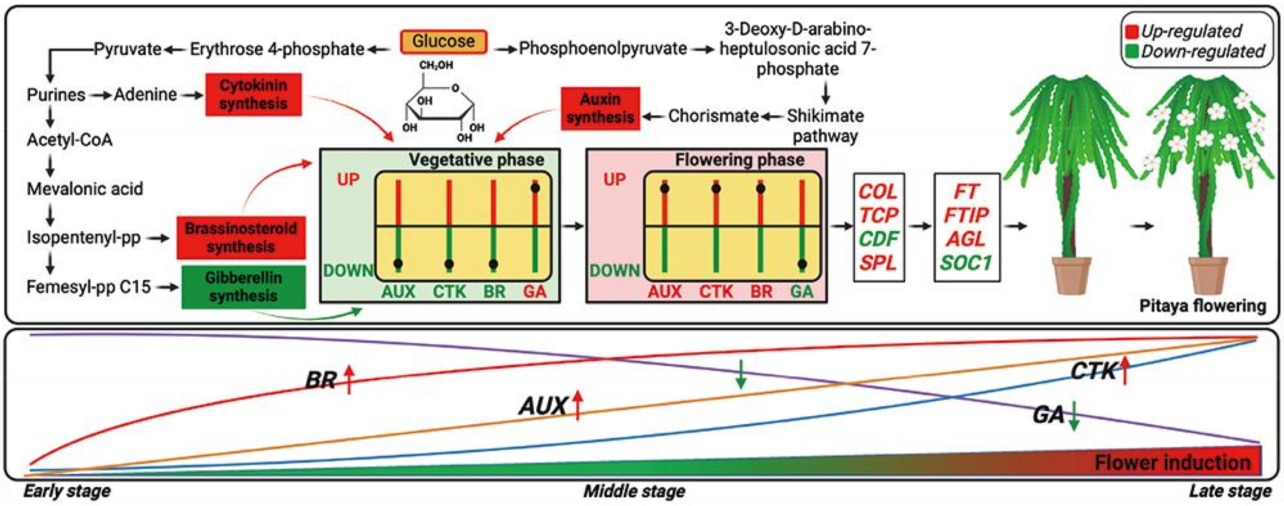

Figure 1 Schematic representation of the regulatory mechanisms through which sugar and hormone signaling activate key transcription factors (TFs) and floral genes in pitaya flowering (Adopted from Shah et al., 2025)

4.2 Ethylene and abscisic acid regulation

Ethylene and abscisic acid (ABA) are two hormones that control flowering in pitaya in different ways. Ethylene usually helps plants flower. In pitaya, it probably does this by changing the way some genes work, making it easier for flower buds to form. Ethylene might also work with other hormones to make sure flowering starts at the right time (Campos-Rivero et al., 2017).

Abscisic acid (ABA) is usually associated with stress or dormancy in plants. In pitaya, abscisic acid also plays a significant role in flowering regulation, serving as a "balancing factor" for ethylene and helping to control the growth time and development mode of flowers. The combined effect of ethylene and abscisic acid constitutes a complex regulatory mechanism, emphasizing that hormonal balance is very important for the optimal flowering conditions of pitaya (Campos-Rivero et al., 2017; Holanda et al., 2021).

4.3 Hormonal interaction models

During the flowering process of pitaya, it is a complex network integrating multiple hormone signals, and hormones do not act alone. Gibberellin, ethylene and abscisic acid all interact with each other and also interact with other signaling systems in plants. For instance, when the content of gibberellin decreased and ethylene and ABA were in equilibrium with each other, this indicated that the hormonal effects during the regulatory process of pitaya were dynamic (Shah et al., 2025).

In flowering regulation, other hormones such as Auxin, Cytokinin and Brassinosteroid also play a role. Several hormones interact to dominate the signaling system, enabling the pitaya to transition from the vegetative growth stage to the reproductive growth stage. Understanding how these hormones work together can help researchers figure out how the flowering mechanisms of pitaya and other similar plants are formed (Shah et al., 2025).

5 Floral Morphology and Functional Adaptation

5.1 Petal and style structures for pollination

The petals and style of the pitaya have undergone fine evolution, which is helpful for pollination. The flowers of *Hylocereus undatus* and *H. polyrhizus*, the red-fleshed pitaya, are larger and open at night. This kind of night-blooming helps attract nocturnal moths and other insects that are active at night. The large and open flowers provide sufficient landing space for pollinators, increasing the probability of successful pollination (Muniz et al., 2019).

The spatial configuration of the stamens and pistils of pitaya flowers plays an important role in the pollination strategy of pitaya. In *H. Undatus* and *H.polyrhizus*, the arrangement of stamens contributes to efficient pollen transfer. The design of the positions of the stamens and pistils enables insects to easily touch the stamens and spread pollen. For instance, when bees or moths shuttle through flowers, they can simultaneously come into contact with both the pollen and the stigma, thereby enhancing pollination efficiency and ultimately achieving an ideal fruit setting rate.

5.2 Arrangement of stamens and pistils

The way stamens and pistils are arranged in pitaya flowers helps improve pollination. In *Hylocereus undatus* and *H. polyrhizus*, stamens are set up so that insects easily touch them when moving around the flower. This means insects like bees and moths can quickly pick up pollen and deposit it onto the stigma, making pollination more effective. This arrangement is particularly helpful for *H. polyrhizus*, which needs insects for successful fruit production (Figure 2) (Muniz et al., 2019).

The structure of pitaya flowers also suits different types of pollinators, both day-active insects like bees (Apis mellifera) and night-active moths. This ability to attract various pollinators improves the chances of pollination, helping the plant produce more fruit. Thus, the placement of stamens and pistils is very important for pitaya flowers (Muniz et al., 2019).

Figure 2 A and B - *Hylocereus undatus* and *H. polyrhizus* flowers respectively. C and D - Dissected flowers of pitaya *H. polyrhizus* showing bracts and reproductive parts. E - Stigma disposition just above stamens. F and G- Dissected flowers showing the arrangement, size and color of the bracts. H and I - Young fruit and fully-developed fruit of *H. undatus* respectively (Adopted from Muniz et al., 2019)

5.3 Pollen structure and fertility

The structural characteristics of pitaya pollen can ensure the fertility and reproduction of the flowers. pitaya pollen can easily stick to the bodies of pollinating insects and effectively reach other flowers. It is crucial that such structures exist in species like *H. polyrhizus*. These plants rely on insect pollination and fruiting and can effectively cross-pollinate (Muniz et al., 2019).

The fertility analysis of pitaya pollen indicates that *H. undatus* lacks biological pollination and can spontaneously bear fruit, while *H. polyrhizus* has limited self-pollination ability. To achieve a high fruit setting rate and form high-quality fruits, it depends on the activities of pollinators, such as *Apis mellifera*. The optimization of pollen structure for its adhesion and vitality is also an important factor affecting fruit yield and quality (Muniz et al., 2019).

6 Floral Scent Biosynthesis and Regulation

6.1 Main scent compounds

pitaya flowers mainly produce a special odor called volatile organic compounds (VOCs). These volatile organic compounds help attract pollinating insects and animals, especially at night. pitaya flowers usually release their strongest scent at night, which matches the active time of night pollinators. In Petunia hybrida, there are the same characteristics as pitaya flowers. The release of volatile compounds follows a circadian rhythm pattern and emits a strong odor at night to attract pollinators (Patrick et al., 2023).

In Pitaya flower, the main volatile organic compounds include benzene compounds and phenylpropanoid compounds, which are the products of floral volatile benzene/phenylpropane (FVBP) metabolic pathway. These compounds come from a special metabolic pathway called FVBP in flowers. Odor compounds attract pollinators, helping plants reproduce successfully and increase the pollination rate (Fenske et al., 2015).

6.2 Key genes in biosynthetic pathways

The biosynthesis of floral substances in pitaya is regulated by the gene network. In petunias, a special gene called LATE ELONGATED HYPOCOTYL (LHY) plays a key role in regulating the timing of volatile substance release. This gene achieves this regulation by controlling the expression of related genes in the FVBP metabolic pathway (Fenske et al., 2015). There may also be a similar system in pitaya flowers, with key transcription factors regulating the floral fragrance synthesis genes and controlling the production of odors

Regulation at the chromatin level, such as histone acetylation, has been shown to mediate diurnal fluctuations of specific metabolites in flowers. Regulation of dynamic changes involving histone acetylation markers is an important mechanism regulating the rhythmic expression of genes related to floral synthesis and release (Patrick et al., 2023; Lv et al., 2024). Similar epigenetic mechanisms may also play an important role in the regulation of pitaya floral synthesis. How pitaya flowers regulate odor production can be studied

6.3 How flowers release scents at the right time

Pitaya flowers probably use their internal biological clock, or circadian clock, to decide when to release scents. This clock helps the flowers synchronize scent release with the activity of nighttime pollinators. In petunia flowers, the circadian clock gene LHY ensures scent compounds are made mostly in the evening, exactly when pollinators are active (Fenske et al., 2015). Pitaya likely uses a similar method to make sure it attracts pollinators efficiently.

Chromatin modifications also affect the release of fragrance from pitaya flowers. Histone acetylation markers (such as H3K9ac and H3K27ac) are dynamically regulated and can affect odor production, and when these markers are removed at night, there is no synthesis of flower substances in the morning (Patrick et al., 2023). In pitaya, this epigenetic regulation may also affect when and how the aroma is released. The timing of fragrance release is often closely related to environmental changes.

7 Flowering and Pollination Interaction

7.1 Main pollinators and their behaviors

Pitaya flowers open at night. This matches the active times of their main pollinators like bats and moths. These pollinators are drawn to the flowers because they have a strong smell and bloom during the night. Flowers close by morning, which fits the lifestyle of these night-time visitors. This night-time blooming helps pitaya plants get pollinated more easily (Xiong et al., 2020; Ye et al., 2021).

How these pollinators behave is very important for pitaya plants to reproduce. Bats can travel far, which helps carry pollen between plants that are far apart. Moths like the flowers’ scent and can visit many flowers in just one night. Understanding how these pollinators behave can help farmers grow better pitaya fruits (Xiong et al., 2020; Ye et al., 2021).

7.2 Synchronicity of flowering and pollinator activity

The flower and the pollinator are active at the same time, which makes pollination more efficient. pitaya flowers bloom at night, when pollinators such as bats and moths are most active. Pollinators find flowers by smell and color, and matching the time can increase the chance of pollination and ensure successful pollination (Xiong et al., 2020; Ye et al., 2021).

The timing of flowering is influenced by a combination of genetic and environmental factors, such as day length and temperature. Such as *HuNIP6; 1* gene can play an important role in regulating flowering time, ensuring that flowering time coincides with pollinator activity. This level of regulation is important for maintaining flowering and pollination synchronization and improving the reproductive rate of pitaya plants (Ye et al., 2021).

7.3 Studies on self- and cross-pollination mechanisms

Pitaya is self-fertile and cross-pollinates, which in effect leads to better fruits and seeds. Cross-pollination mixes the genes of different plants together, producing genetic diversity that is better adapted to the environment. Pollinators play an important role in pollen transport between different plants (Xiong et al., 2020; Ye et al., 2021).

Self-pollination is possible, but fruit setting rate and fruit quality are lower than cross-pollination, *HuNIP6; 1* gene will affect the time and duration of pitaya flower opening, and thus affect self-pollination or cross-pollination.In-depth understanding of these pollination methods will improve the yield and quality of pitaya (Ye et al., 2021).

8 Multi-omics Methods in Flowering Research

8.1 Discover important pathways using transcriptomics

Transcriptomics can help understand how genes control the flowering of pitayas. Through RNA sequencing, researchers discovered that many genes changed their activity during the flowering period. Give the pitaya extra light in winter. It discovered important genes related to energy utilization and plant hormones, such as CONSTANS-LIKE and flowering site T, which directly affect when pitaya flowers (Xiong et al., 2020). Furthermore, researchers have noted that sugar and hormone signals play an important role. The key genes involved in starch and sugar metabolism, as well as hormones such as auxin, cytokinin and brassinol-steroids, are important for flower bud formation (Shah et al., 2025).

Other transcriptomic studies focus on how genes control each stage of peanut growth. In red-fleshed pitayas, researchers studied the nine stages of flower development. They discovered genes related to hormone signaling, gene activity and sugar transport. Some key hormone-related genes, such as those controlling indole-3-acetic acid, abscisic acid and ethylene, have undergone significant changes, indicating that they are important for the parts that form flowers (Wu et al., 2022). These results help us understand the complexity of pitaya flowering and provide ideas for future research to improve flowering and crop yields.

8.2 Metabolomics linking scent and flowering time

Metabolomics can study chemical changes in plants, giving researchers a new perspective on the link between pitaya flowering and odor production. During the transition from vegetative growth to reproductive growth, important changes occurred in carbon and nitrogen levels, nitrogen content decreased while carbon content increased, changing the balance between carbon and nitrogen. Influence genes involved in sugar production, transport, and response to daylight and temperature to help control flowering timing (Shah et al., 2024).

Metabolomics can also be used to study the relationship between odor production and flowering time. The synthesis of floral fragrances is related to the timing of flower opening, pitaya flowers open at night, and sugars interact with hormone signaling pathways that regulate odor production and the timing of flowering. During the final stages of bud formation, sugars and starches accumulate, providing materials for the production of odors that attract pollinators and aid reproduction (Shah et al., 2025).

8.3 New research on epigenetics and miRNA

The role of epigenetic and miRNA regulation in the flowering of Pitaya can be understood more about the flowering process of pitaya. Epigenetic modifications, such as DNA methylation and histone acetylation, play an important role in the regulation of gene expression during flower development. The relevant studies in pitaya are still limited, but some studies have shown that such epigenetic modifications may affect key flowering genes and their signaling pathways, and change the flowering stage and flower morphological characteristics.

miRNAs are small RNA molecules that also help control flowering. They influence genes after they are copied from DNA, either by breaking down the RNA or stopping it from making proteins. In other plants, miRNAs control hormone pathways and development timing, both important for flowering. Although miRNA studies in pitaya are just starting, research from related plants gives clues about how miRNAs might influence pitaya flowering.

9 Perspectives and Conclusion

The flowering process of pitaya is complex, and in this process, the genetic regulatory mechanism is of great significance. Researchers identified some key genes (*CONSTANS-LIKE* and *FLOWERING LOCUS T*) that are highly active when flower buds start to grow. In addition, *HuNIP6* was also discovered; The gene *HuNIP6;1*, a aquaporin, affects the flowering time by turning off other genes that delay flowering. These genes are of great help in clarifying the genetic mechanism of pitaya flowering.

In addition to genetic factors, whether environmental factors play an important role. When pitaya is planted in the short day season, other additional light sources can be used to promote flowering. Environmental factors can interact with genes that sense day length and hormone signals, and the fact that pitaya flowers bloom at night suggests that flowering rhythms are closely related to the environment, an area that still needs further research.

Understanding the flowering mechanism of pitaya can increase its yield and help breed better varieties. Identifying key genes and pathways (such as sugar signaling and plant hormone signaling pathways) can help explain how flower buds start to grow. In addition, understanding what characteristics of the flower (such as ultraviolet light absorption) attract pollinators can help guide breeding decisions to make pitaya flowers more accessible for pollination, which will be of great help in improving the yield and quality of pitaya in the future.

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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