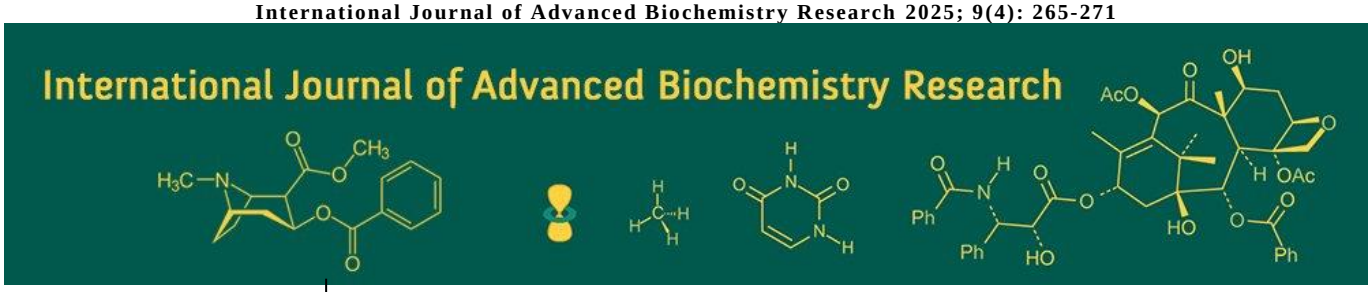

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Advancements in taxonomy, cytology, floral, and pollination biology of dragon fruit: Strategic insights for crop improvement and sustainable production

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Abstract
Dragon fruit has emerged as a commercially valuable crop due to its nutritional benefits, adaptability to diverse environments, and growing market demand. Characterized by its nocturnal flowering behavior and complex pollination mechanisms, optimizing its floral biology is crucial for improving fruit yield and quality. Recent advances in dragon fruit research have extensively explored cytological aspects and applied modern genomic tools for crop enhancement. This review gives a brief botanical profile based on updated taxonomic information. It also provides a comprehensive analysis of flowering biology, pollination strategies and offseason production. By incorporating the latest taxonomic updates and integrating theoretical and applied perspectives, this study serves as a valuable resource for researchers, breeders, and growers aiming to optimize dragon fruit productivity and ensure long-term agricultural sustainability.

Keywords: Taxonomy, *Selenicereus*, anthesis, cross-pollination, self-incompatibility

1. Introduction
Dragon fruit (*Selenicereus* spp.) is one of the world's most widely popular exotic fruit crops. It was initially unfamiliar to many parts of the world, but now every metropolitan market of several countries witnessing the fruit. With the surge in popularity, nutritional importance, and widespread cultivation worldwide, the dragon fruit is known as the wonder fruit of the 21st century. Widespread popularity could be attributed to its striking appearance, characterized by a vivid complexion, and its luscious, juicy pulp containing appealing black seeds that are pleasing to consume (Le Bellec *et al*., 2006) [29]. During the 20th century, it was confined to America and regions of its origin, but at dusk and dawn of the 21st century, the crop was gradually spread across several countries of different continents. From its center of origin, it has spread to several countries, viz. Australia, Cambodia, China, Colombia, Ecuador, Guatemala, Hawaii, Indonesia, Israel, Malaysia, New Zealand, Peru, The Philippines, Taiwan, Thailand, Spain, Sri Lanka, and Vietnam (Ahmad *et al*., 2019) [1]. Surprisingly, dragon fruit become an important commercial crop in southeastern countries like Vietnam, Malaysia, and Thailand. In the last decade, it has drawn much attention from Indian growers due to its high monetary and nutritional values besides attractive vibrant skin (red/pink and yellow) and flesh (white and red/pink) colors, rich antioxidant properties and anti-inflammatory benefits (Trivellini *et al*., 2020) [57]. With its ease of cultivation, early yield, resilience, uniqueness, and numerous health and medicinal benefits, dragon fruit is emerging as an up-and-coming crop, even suitable for degraded land and abiotic stress-prone regions providing the required minimal resources to support its growth. The hardiness of the CAM plant, along with its capacity to withstand high temperatures, has enabled its cultivation in diverse agro-climatic zones, particularly in challenging environments like semi-arid regions characterized by prolonged periods of soil water scarcity and elevated temperatures (Sosa *et al*., 2020) [50]. As a result, it is gaining significant appreciation among growers and consumers alike. While the initial cost of establishing dragon fruit cultivation may be relatively high due to the necessity of trellises for support, other agronomic practices associated with the initial crop establishment are cost-effective, leading to low maintenance

expenses. One of the most significant advantages of cultivating dragon fruit is its prolonged lifespan. Once planted, dragon fruit plants can thrive for approximately 20 years, providing a consistent and sustainable source of fruit production. Moreover, a single hectare of land can accommodate 1000 to 2000 dragon fruit plants, depending on the planting methods and spacing.

Despite the potential and opportunities offered by dragon fruit cultivation, several challenges are associated with its commercial cultivation. Though the cultivation of dragon fruit is expanding across different regions of the world, the production of this fruit is not consistent and stable throughout the flowering season. Consequently, the crop is not sustaining in several countries despite its boom in a short period span. This inconsistency can be attributed to the lack of region-specific and season-specific agronomic practices to optimize crop production and management and also the lack of regulatory framework or guidelines for border control measures, which results in unethical export or import of the planting materials of unknown diverse clonal varieties or hybrids without knowing their performance and quality. As a result, farmers face various challenges, including sunburn, yellowing of stems, the emergence of new pests and diseases, and flower and fruit drops, the causes of which are often difficult to identify. Specifically, flower and immature fruit drops are observed during the rainy months as flowering coincides with the rainy season. The heavy and continuous rainfall can disrupt pollination, leading to failed fertilization and reduced fruit size (Boraiah *et al*., 2021) [4]. Interestingly, such rain-induced yield losses incidences were reported more frequently in the white-fleshed varieties mostly belonging to *S. undatus*. This could be due to the floral traits or blooming behavior of the species or varieties. Supplemental lighting is a valuable technology for farmers to enhance production and meet the growing consumer demand for dragon fruit. Environmental manipulation to induce flowering presents a promising approach for ensuring market availability during shorter days. For this, it is crucial to understand the floral biology of the crop.

However, the limited availability of consistent and reliable information on the flowering behavior and pollination requirements of dragon fruit, especially outside of its native geographic area, has hindered the full exploitation of this crop in various regions of the world, including India. Further, published information is scarce on dragon fruit in India.

With this background, this review article aimed to give a brief botanical profile based on updated taxonomic information and to identify gaps in the current knowledge of the floral and pollination biology of dragon fruit, which may aid in the development of pollination management, especially for dragon fruit grown outside their native distributions. The review also aims to study the behavior of floral visitors in dragon fruit, *Selenicereus*. In the end, the article discussed the importance of developing demand-need-based varieties and a road map for crop improvement.

2. Botanical profile: Understanding the crop origin, evolution and cytology

According to Le Bellec *et al*. (2006) [29], most *Selenicereus* species are native to Latin America, particularly Mexico and Colombia, a conclusion also supported by Barthlott and Hunt (1993) [3] and Pimienta-Barrios and Castillo (2002) [45]. A comprehensive overview of the origin of different dragon fruit species is provided in Table 1. The scientific commercial cultivation and improved understanding of its taxonomy have contributed to the fruit's increased popularity, both as a fresh commodity and a value-added product in the global market.

Table 1: Dragon fruit species and their geographic origins

Species	Colour	Origin
Selenicereus undatus (formerly *H. undatus*)	Red skin and white pulp	Columbia, Mexico, and South America (Bravo-Hollis, 1978) [6]
Selenicereus costaricensis (formerly *H. costaricensis*):	Dark magenta peel and violet-red flesh.	Costa Rica and Nicaragua (Fouque, 1972) [21]
Selenicereus monacanthus (formerly *H. monacanthus* or *H. polyrhizus*):	Red skin and red pulp	Costa Rica, Nicaragua and the regions around Panama (Anderson, 2001) [2]
Selenicereus megalanthus (formerly *H. megalanthus)*	Yellow skin and white pulp	Mexico, region of Colombia, Peru, Bolivia, Ecuador, and Venezuela (Fouque, 1972) [21]
Selenicereus ocamponis	Yellow skin and red pulp	Brazil, Colombia, and Uruguay (Fouque, 1972) [21]

Dragon fruit, scientifically known as *Hylocereus undatus* and first documented in Britton's *Flora of Bermuda* (Britton, 1918) [8], is the second most commercially significant cactus species after *Opuntia ficus-indica*. The cactus family comprises 1,500 to 2,000 species, including 16 *Hylocereus* species, mostly with creamy white flowers, except *H. extensus* and *H. stenopterus*, which have rose-pink and red petals.

Historically, dragon fruit species were classified into two genera, *Hylocereus* and *Selenicereus*. However, molecular phylogenetic studies in 2017 revealed that *Hylocereus* species were nested within *Selenicereus*. As a result, the genera were merged under *Selenicereus*, which now includes 33 recognized species (Korotkova *et al*., 2017) [28]. Detailed taxonomic classification of dragon fruit is given in Table 2.

The taxonomy of dragon fruit has historically been complex and disorganized, with the same species often classified under different names. Extensive intra-and inter-specific hybridization has further complicated the identification of species and varieties, leading to significant taxonomic confusion on a global scale. This hybridization has resulted in substantial morphological diversity.

Table 2: The taxonomic classification of dragon fruit

Kingdom	Plantae
Sub kingdom	Tracheobionta (vascular plants)
Super division	Spermatophyta (seed plants)
Division	Magnoliophyta (flowering plants
Class	Magnoliopsida (dicotyledons)
Order	Caryophyllales
Family	Cactaceae
Subfamily	Cactoideae
Genus	Selenicereus
Species	*Selenicereus undatus* (Haworth) D.R.Hunt

Sources: Britton and Rose (1963) [7]; Korotkova *et al*. (2017) [28].

The plant genome serves as the basis for exploring gene functions, population genetics, species evolution, and molecular breeding. Therefore, a high-quality genome is essential for comprehending the mechanisms underlying various biological traits in plants. In 2021, two reference genomes of *S. undatus* were released, providing a valuable resource for advancing dragon fruit research (Chen *et al*. 2021) [11]. In the Cactaceae family, the monoploid chromosome number is x = 11. Most species classified under the genus *Selenicereus*, derived from the Greek words "Selene" (goddess of the moon) and "Cereus" (referring to its nocturnal flowering habit), are diploid, possessing 2n = 2x = 22 chromosomes. However, *S. megalanthus* (previously *H. megalanthus*) is a tetraploid species with 2n = 4x = 44 chromosomes. This close genetic relationship among dragon fruit highlights the potential for generating diploid hybrids through interspecific homoploid crosses (2n × 2n) (Lichtenzveig, 2000) [32].

3. Botany

Dragon fruit is a rapidly growing, perennial climber that relies on mechanical support due to its semi-epiphytic nature (Korotkova *et al*., 2017) [28]. Its fleshy, triangular stems, called cladodes, may have up to five sides with wavy wings and 1 to 3 spines, though some varieties lack spines altogether (Gunasena *et al*., 2006) [23]. The stems have a waxy coating that helps retain moisture, and instead of true leaves, the plant has thorns, which are modified leaves. Suited to arid environments, it uses the Crassulacean Acid Metabolism (CAM) pathway to fix carbon dioxide at night, reducing water loss. The plant has both aerial and underground roots that facilitate climbing and water absorption.

Dragon fruit produces large, fragrant, nocturnal flowers that emerge from mature shoots, with species-specific differences. *S. undatus* has light green buds with greenish outer perianth segments and white inner segments, while *S. polyrhizus* features reddish outer segments with red-edged bracts. *S. costaricensis* resembles *S. undatus* but has yellowish outer perianth segments and a stronger fragrance (Pushpakumara *et al*., 2005) [47]. The plant typically flowers 4 to 7 times per year. The fruit is an oblong to ovoid fleshy berry with prominent scales, measuring 6 to 12 cm in length and 4 to 9 cm in diameter. Its peel color varies, appearing pink, red, or yellow in the case of *S. megalanthus*, with the pulp being either white or red, containing numerous small, black edible seeds (Merten, 2003) [33]. Fruits usually weigh between 350 and 400 g, but they can grow as large as 800 g depending on species.

4. Floral and pollination biology

4.1 Reproductive phenology

Dragon fruit undergoes a distinct reproductive period, transitioning from vegetative growth to reproductive development, which significantly impacts yield and fruit quality. The reproductive phase varies across species and climatic conditions, influencing flowering cycles, duration, and fruit maturation. Weiss *et al*. (1994) [60] reported two to three flowering waves from May to October, while N'Guyen (1996) [38] observed seven to eight flushes in *S. costaricensis* and five to six in *S. undatus*. In Sri Lanka, the reproductive phase extends from April to November with four to six cycles (Pushpakumara *et al*., 2005) [47], whereas in Brazil, flowering begins in spring and continues until autumn. *S. polyrhizus* flowers from November to May in Brazil, while in Mexico, five to seven cycles occur between June and October (Osuna-Enciso, 2016) [44]. Boraiah *et al*. (2021) [4] observed that *S. undatus* flowers from April to October, whereas *S. polyrhizus* blooms from May to September with five to six cycles. The duration of reproductive phases varies, with bud initiation to anthesis taking 13-35 days depending on species and location (Pushpakumara *et al*., 2005; Boraiah *et al*., 2021) [47, 4]. Anthesis to maturity ranges from 28 to 90 days, with shorter durations in Israel and Vietnam (Mizrahi *et al*., 2002) [34] and longer periods in Mexico and Brazil (García-Suárez *et al*., 2007) [22]. The entire reproductive cycle spans approximately 50-166 days, with *S. megalanthus* requiring the longest duration. Understanding these reproductive traits is crucial for optimizing yield and developing effective cultivation strategies for dragon fruit.

4.2 Floral morphology

Morphological traits are essential for distinguishing plant germplasm and species, aiding in taxonomic classification, breeding programs, and varietal improvement (Ercisli and Esitken, 2004) [20]. Dragon fruit flowers are hermaphroditic, nocturnal, bell-shaped, tubular, actinomorphic, and pedunculated, with variations in color (Joanna and Ding, 2021; Zee *et al*., 2004; Mizrahi *et al*., 1999; Muniz *et al*., 2019) [12, 62, 35, 37]. Flower dimensions vary, with buds measuring ~25.2 cm before anthesis and reaching ~27.2 cm in length and ~28.8 cm in width when fully open, while Le Bellac (2006) [29] recorded bud lengths of ~29 cm. Accessory floral organs include sepaloid tepals, with ensiform types measuring ~12 cm long and 1 cm wide, and petaloid tepals, consisting of 24 lance-ovate inner tepals (white) and five lanceolate outer tepals (white-yellowish), both around 10 cm long (Joanna and Ding, 2021) [12]. Functional floral structures include a basal ovary, numerous cream-colored stamens attached to the perianth tube apex,

and a creamy white stigma with ~15 lobes (Le Bellac, 2006) [29]. Weiss *et al*. (1994) [60] reported a 2 cm spatial difference between stigma and anthers in *Selenicereus* spp. The anthesis in dragon fruit starts at 6.30 PM in the evening, completely blooms between 9.00 PM-12.00 AM, starts closing 7.00 AM onwards, partially closes at 9.00 AM and starts withering 10.30 AM as sunshine increases (Boraiah *et al*. 2021) [4].

4.3 Floral physiology

Floral physiological parameters like anther dehiscence, viability, germinability, stigma receptivity play major role in pollination and fertilization. Pollen dehiscence in dragon fruit occurs at night, with anthers beginning to release pollen while flowers are still closed, and a significant amount is available by 16:00 h, well before the flowers open at 19:00 h (Centurion-Yah *et al*., 2008; Muniz *et al*., 2019) [61, 37]. Pollen viability plays a crucial role in reproductive success and plant breeding programs, especially in fruit crops requiring supplementary pollination (Dos Santos *et al*., 2020) [19]. Pollen viability peaks at anthesis, reaching 90-94 %, but declines by the following evening as flowers close (Weiss *et al*., 1994) [60]. Pollens collected 12-10 hours before anthesis are non-viable, while the highest activity is observed around 22:00 h (Li *et al*., 2020) [30]. In *S. undatus*, pollen remains viable for up to 18 hours after anthesis, with the highest viability within 14 hours, making early morning pollination before 10:00 AM optimal (Boraiah *et al*., 2021) [4]. Pollen germination rates exceed 92.5 % from 2 hours before to 10 hours after blooming, ensuring successful fruit set (Li *et al*., 2022) [31]. Pollen viability increases after 21:00 h, peaking between 02:00-04:00 h, making early morning ideal for collection and pollination (Del Ángel-Pérez *et al*., 2022) [17]. Stigma receptivity extends from 20:00 h until flowers close at 07:00 h, or until 09:00 h on cloudy days (Muniz *et al*., 2019; Moreira *et al*. 2022) [37, 36]. Stigmas become receptive two hours post-anthesis, leading to a 93.3 % fruit set, while pollination four hours before anthesis yields only 71.7 % (Li *et al*., 2020) [30].

4.4 Mode of pollination and pollination mechanisms promoting mode of pollination

Pollination in dragon fruit involves the transfer of pollen from the anther to the stigma, occurring either through self-pollination or cross-pollination, with success influenced by flower structure, pollen availability, and timing. While self-pollination is common, it often results in lower fruit quality and yield (Moreira *et al*., 2022) [36]. Pollination is facilitated by both biotic agents, such as insects, bats, and hawkmoths, and abiotic agents like wind (De Brito & De Souza, 2020) [16]. *S. polyrhizus* exhibits a nocturnal anthesis pattern, emitting a strong musky scent that attracts primary pollinators like bats, which feed on nectar and pollen, confirming its chiropterophilous pollination system (Weiss *et al*., 1994; Valiente-Banuet *et al*., 2007; Joanna & Ding, 2021) [59, 32, 12]. Both nocturnal and diurnal visitors play a role in its mating system, enhancing cross-pollination (Lichtenzveig *et al*., 2000; Valiente-Banuet *et al*., 2007) [32, 59]. Dragon fruit varieties exhibit diverse pollination mechanisms, including allogamy (cross-pollination), autogamy (self-pollination), or a combination of both, depending on genetic factors and self-incompatibility (Pio *et al*., 2020; Weiss *et al*., 1994) [46, 60]. While many clones are self-pollinated, some require cross-pollination to overcome self-incompatibility and ensure fruit set (Nerd & Mizrahi, 1997) [39].

Breeding systems already described show a wide variety of compatibility systems (Weiss *et al*., 1994) [60]. Self-incompatibility of the plant is evidenced by spatial segregation of the sexual organs (Weiss *et al*., 1994) [60] and dry-type stigma. Following self-pollination, pollen germination occurs on the stigma; however, the growth of the pollen tube is obstructed within the style, demonstrating the characteristic gametophytic self-incompatibility (GSI) in dragon fruit (Qu *et al*., 2017) [48]. *S. monacanthus* is a self-incompatible diploid, while *S. megalanthus* is a self-compatible tetraploid. Some species show partial self-compatibility (Lichtenzveig *et al*. 2000) [32], with occasional self-fruitfulness observed in *S. monacanthus* (Tel-Zur, 2011) [55].

4.5 Pollinating agents

The relationship between flowers and pollinators is primarily established through floral incentives such as nectar, pollen, oil, resin, and water, which fulfill pollinators' nutritional, reproductive, or shelter needs. Pollination occurs through biotic agents, including insects and animals, and abiotic agents, such as wind and water (De Brito & De Souza, 2020) [16]. The evolution of hypanthium in Cactoideae facilitated the development of long floral tubes, attracting a diverse range of pollinators and leading to varied pollination strategies (Schlumpberger, 2012) [41]. *Hylocereus polyrhizus* exhibits pollination by both nocturnal and diurnal visitors, with nocturnal anthesis accompanied by a strong musky scent that attracts bats and hawkmoths, its natural pollinators (Weiss *et al*., 1994; Lichtenzveig *et al*., 2000; Valiente-Banuet *et al*., 2007) [60, 59, 32]. Bats are considered the primary pollinators of *H. polyrhizus*, collecting nectar and pollen, which aligns with chiropterophilous pollination traits (Valiente-Banuet *et al*., 2007; Joanna & Ding, 2021) [60, 12]. However, due to limited nighttime pollinators, these species have adapted to generalist pollination strategies by keeping flowers open past sunrise to attract diurnal pollinators. Butterflies from the *Sphingidae* family, such as those from the *Maduca* genus, also serve as pollinators (Daubresse, 1999) [18]. Bees, particularly *Apis cerana*, *A. florea*, and *A. dorsata*, play a role in pollinating dragon fruit, especially in the early morning hours (Pushpakumara *et al*., 2005) [47]. Some studies suggest that honey bees may not be efficient pollinators of dragon fruit due to the large flower size and floral structure, which reduces their direct contact with the stigma (Weiss *et al*., 1994; Merten, 2003) [60, 33]. Further studies are needed to assess the efficiency of various honey bee species, including the Asian and Africanized honey bees, in pollinating dragon fruit flowers.

5. Insights for enhancing the production via efficient pollination management and offseason production

Efficient pollination management in dragon fruit involves manual pollination and introducing managed honeybee colonies to enhance fruit set (Table 4). For self-incompatible varieties, manual cross-pollination is essential for improving yield and quality. Artificial pollination using diverse genotypes and species has shown promise in increasing fruit set, fruit weight, and quality (Tran *et al*., 2015) [56]. Supplementary cross pollination with suitable pollen enhance fruit size (Boraiah *et al*., 2021) [4].

As a long-day plant requiring at least 12 hours of light, dragon fruit benefits from night-breaking techniques to extend the harvesting period and enable off-season production (Hung & Huong, 2015; Jiang *et al*., 2012; Zee *et al*., 2004) [24, 26, 62]. Supplemental lighting between 10:00 PM and 2:00 AM induces winter flowering, leading to larger, sweeter, high-value fruits (Jiang *et al*., 2012) [26]. PGR application and microclimate modifications also help extend the flowering season and induce off-season flowering. PGRs such as Cytokinins, particularly trans-zeatin and isopentenyladenine, play a key role in flower initiation, with peaks occurring before flower bud development in dragon fruit. Exogenous cytokinins promote fruit bud initiation (Stephan, 1997) [52]. CPPU accelerate flowering, while GA_3 delays it, allowing flexibility in harvest timing (Saradhuldhat, 2019) [50].

6. Insights for crop improvement to sustain and gear up the production

Sustainable dragon fruit production depends on genetic improvement for high-yielding, disease-resistant, and climate-resilient varieties. Farmers primarily use cuttings for propagation, ensuring uniformity and early production. However, this limits genetic diversity, which is crucial for long-term crop improvement. Seed propagation introduces variability, allowing selection for superior traits, while interspecific hybridization facilitates the development of new varieties with enhanced fruit quality (Tel-Zur *et al*., 2004) [54]. Hence, development and standardization of seed propagation is crucial (Boraiah *et al*., 2024) [5].

To assess germplasm diversity, molecular markers such as RAPD and ISSR have been widely used (Tao *et al*., 2014) [53], alongside morphological characterization based on cladode, flower, and fruit traits (Ortiz Hernández & Carrillo Salazar, 2012) [43]. Dragon fruit's self-incompatibility (SI) results in low natural fruit set, necessitating biological and artificial pollination, which increases labor costs and limits commercial production. Breeding and biotechnology offer solutions to overcome SI. Hybrid cultivars with improved self-compatibility can be developed through conventional breeding and marker-assisted selection (MAS). CRISPR-Cas9 can target S-locus genes to enhance self-compatibility, improving fruit set and quality. Advanced breeding techniques like cisgenesis and CRISPR/Cas can also enhance disease resistance and stress tolerance, supporting sustainable cultivation (Campa *et al*., 2023) [9].

7. Conclusion and future perspectives

Advancements in the taxonomy, cytology, and reproductive biology of dragon fruit (*Selenicereus* spp.) provide a solid foundation for enhancing its productivity and commercial potential. Understanding its unique nocturnal flowering behavior and pollination mechanisms has paved the way for improved pollination management strategies. Recent research highlighting self-incompatibility and the effectiveness of cross-pollination emphasizes the importance of selecting appropriate pollination methods to optimize fruit set and quality. Furthermore, the integration of genomic tools and cytological studies offers new opportunities for developing self-compatible and resilient cultivars. Integrating efficient pollination strategies, supplemental lighting, and PGR applications ensures consistent production, improved fruit quality, and better market availability.

This comprehensive knowledge serves as a valuable resource for researchers, breeders, and growers, facilitating informed decision-making to enhance dragon fruit productivity and meet the demands of a growing global market. Future research should focus on genetic advancements to enhance self-compatibility, conservation of key pollinators, and refinement of manual pollination techniques.

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