Review Article

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Floral biology, pollination behaviour and pollinators in bael (*Aegle marmelos*) in rainfed semi-arid conditions - A review

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ABSTRACT

Bael a cross-pollinated fruit crop, relies heavily on effective pollinizers to enhance fruit set, yield, and quality, particularly in commercial cultivars and self-incompatible varieties. Pollinizers play a pivotal role in supporting reproductive success by providing abundant, viable, and compatible pollen that synchronizes with the flowering period of commercial varieties. This synchrony not only ensures successful pollination but also enables pollen storage for future use. The phenomenon of herkogamy further facilitates cross-pollination in bael, emphasizing the need for optimal pollinizer arrangements in orchards. Despite their importance, the role of pollinizers is often underestimated by fruit growers due to limited awareness and insufficient scientific information. This review consolidates existing knowledge on pollination biology, the ecological role of pollinizers, and the management practices required to optimize pollinator services in bael cultivation, particularly in rainfed semi-arid conditions. By addressing critical knowledge gaps, this study underscores the necessity of maintaining recommended pollinizer ratios and highlights strategies for enhancing pollination efficiency to achieve sustainable productivity in bael orchards.

Introduction

Bael (*Aegle marmelos*), a subtropical tree belonging to the Rutaceae family, is an integral part of Indian culture and agriculture. Commonly referred to as bilva, golden apple, Bengal quince, and Maredu, this species holds deep religious significance in Hindu traditions, where it is often called the "tree of Shiva" (*Shivaduma*) (Neeraj *et al.*, 2017). Its trifoliate leaves are symbolic in Hindu philosophy, representing sacred triads such as the Trimurtis (Brahma, Vishnu, Shiva) and the three Gunas (Satva, Rajo, Tamo). Bael demonstrates remarkable ecological adaptability, thriving in drought-prone regions, nutrient-deficient soils, and saline or sodic conditions. It also shows resilience to various pests, diseases, and climatic extremes, making it a crucial species for semi-arid and rainfed ecosystems. The tree flourishes in dry forests and semi-arid plains at elevations of up to 1200 m above sea level and can withstand both arid environments and high rainfall, underscoring its potential as a sustainable crop for challenging agricultural landscapes (Bobade *et al.*, 2020; Singh *et al.*, 2021). Bael (*Aegle marmelos*), a versatile subtropical tree, is renowned for its ability to thrive under extreme and varied conditions. It grows robustly and bears fruit even on challenging soils, such as the limestone soils of southern Florida and swampy, alkaline, or stony soils with a

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pH range of 5 to 10 (Singh *et al.*, 2019e). The tree requires a distinct dry season for fruit production, showcasing its resilience in environments unsuitable for other fruit crops. Beyond its adaptability, bael contributes significantly to environmental health by acting as a natural air purifier, releasing higher oxygen levels than many other tree species (Mali *et al.*, 2020).

Bael holds immense medicinal value, with nearly every part of the tree-roots, flowers, leaves, fruits, and bark-utilized in traditional herbal medicine systems, including Siddha (Rajasekaran *et al.*, 2009). Indian medicinal plants, including bael, are recognized as rich reservoirs of pharmacologically active compounds widely used to treat various ailments (Tiwari *et al.*, 2018). Moreover, through advanced post-harvest technologies, bael fruits are transformed into diverse value-added products such as toffees, jams, ice creams, candies, and juices. These innovations minimize post-harvest losses and enhance shelf life and market value, providing a sustainable source of income for farmers (Singh *et al.*, 2019e).This combination of ecological resilience, medicinal significance, and economic potential underscores bael's vital role in sustainable agriculture, health, and livelihoods.

Approximately 80% of cultivated crops worldwide rely on cross-pollination for the production of fruits, seeds, and vegetables. This critical process not only enhances crop yield and quality but also reduces the time between flowering and fruit setting, while protecting developing fruits from pests, diseases, and agro-chemicals. The present study examines pollinator abundance and pollination dynamics in bael (*Aegle marmelos*), a predominantly cross-pollinated crop where only 5% of flowers are self-pollinated, and 95% depend on cross-pollination. Bael flowers are entomophilous, with pollination primarily facilitated by insect pollinators, including honey bees (*Apis dorsata*, *Apis mellifera*), hoverflies, yellow wasps, beetles, weevils, carpenter bees, black ants, and butterflies. Among these, bees are recognized as the most efficient and legitimate pollinators, while other organisms contribute incidentally by feeding on nectar and transferring pollen between flowers (Satapathy and Chandra, 2017).Pollinizers and pollinators play a pivotal role in various floral biological activities of bael, such as pollination, fruit set, fruit retention, quality, shelf life, and harvesting period. These activities are directly or indirectly influenced by the interaction of pollinators, pollinizers, and environmental factors, which collectively determine the yield and quality of the crop (Saroj *et al.*, 2021). Like many other cross-pollinated horticultural crops in semi-arid regions, bael requires effective pollinizers (pollen sources) to achieve commercially viable fruit production and high-quality yields.

Characteristics of ideal pollinizer variety

Not all male plants that produce pollen qualify as effective pollinizers. For a pollinizer variety to be considered ideal, it must meet specific criteria:

Flowering Synchrony: The flowering period of the pollinizer must align with that of the commercial variety, with an extended bloom period to ensure maximum overlap.

Pollen Viability and Compatibility: It should produce an abundant quantity of viable pollen grains that are compatible with the commercial variety, maintaining consistent pollen production throughout the flowering period.

Presence of Pollinators: The orchard should support an active population of bees and other insect pollinators during the bloom period to facilitate effective pollen transfer.

Proximity: The pollinizer trees must be strategically placed in proximity to the commercial variety to maximize pollination efficiency.

Pollen Storage: The pollen from the pollinizer should be suitable for storage, allowing its use for future pollination of specific flowers.

Marketable Yield: The pollinizer variety should also produce fruit of marketable quality, adding value to its inclusion in the orchard.

These characteristics ensure that the pollinizer contributes effectively to fruit set, yield, and quality, supporting the commercial success of cross-pollinated crop systems.

Essential Conditions for Effective Pollinizers in Orchard Development

The effectiveness of a pollinizer in ensuring successful orchard development depends on fulfilling specific conditions. These include synchrony in flowering with the main crop variety, production of viable and compatible pollen, strategic placement within the orchard, and the presence of active pollinators during the bloom period. Adherence to these conditions is crucial for optimizing fruit set, yield, and overall orchard productivity.

Role of Pollinizers in Self-Incompatible Cultivars: For self-incompatible cultivars or species, pollen is typically sourced from closely related, compatible species to facilitate fruit production. In such cases, the presence of effective pollinizers plays a critical role in significantly enhancing yield.

Impact on Pollination and Fertilization: Pollinizers improve the efficiency of the pollination and fertilization processes, leading to increased yields with larger, well-formed, and higher-quality fruits.

Contribution to Yield: By increasing the number of fruits per tree, pollinizers contribute directly to higher overall yields in orchards.

Genotypic Influence on Fruit Quality: Research highlights that fruit size, shape, and quality attributes are directly influenced by the genotype of the pollen, underscoring the importance of effective pollination in achieving superior fruit characteristics.

Economic Benefits of Pollinizers: Pollinizer varieties consistently produce high-value commercial crops, offering growers a reliable source of income year after year.

Pollinizers in Hybridization Programs: Hybridization, involving cross-pollination between flowers of different species or various breeding lines and genotypes, requires a dependable donor pollinizer. This is essential for the success of breeding programs aimed at varietal improvement.

Floral biology: Anthesis and Dehiscence time

Bud Emergence Across Varieties: Bud emergence in bael (*Aegle marmelos*) varieties initiates at different times, extending overall from April to late July (Singh *et al.*, 2006a). This variability underscores the genetic diversity among cultivars.

Extended Flowering Period and Pollinator Stability: Varieties with prolonged flowering periods serve as long-term floral resources, while the flowering patterns and phenology of different cultivars significantly influence ɛp roductive success and help sustain stable pollinator populations (Singh *et al.*, 2010b; Singh *et al.*, 2016b).

Petal in Genotypes: Variations in petal morphology, including an abnormal number of petals, are commonly observed across nearly all bael genotypes, reflecting underlying genetic or environmental influences. Usually 4 to five petals are common in almost all genotypess, sometimes abnormal petals may be seen in very few genotypes (Singh *et al.*, 2018a; Singh *et al.*, 2019b).

Anthesis and Anther Dehiscence Timing: Anthesis in bael begins at 6:00 AM and continues until 2:00 PM, with peak flower opening occurring between 8:00 and 12:00 PM. Observations reveal that anthesis and anther dehiscence occur early in the morning (5:30-8:30 AM) under conditions of low temperature and high humidity (Singh *et al.*, 2019b).

Flower Opening Dynamics: During anthesis, flowers exhibit variations in petal opening patterns. Some flowers open all petals simultaneously, while others open sequentially, taking 45-60 minutes to fully open. The duration of this process can vary among flowers within the same genotype, highlighting phenotypic diversity (Singh *et al.*, 2019a).

Post-Anthesis Changes in Floral Organs: Within 30 minutes of anthesis, the anthers and floral organs began to shrink and gradually turned brick red, a process that progressed as dehiscence occurred (Singh *et al.*, 2011b; Singh *et al.*, 2016i).

Bud Opening Patterns in Inflorescences: The sequence of bud opening within the inflorescence varied among varieties. In most cases, buds located on the lower side of the inflorescence opened earlier than centrally positioned buds. However, some varieties exhibited a reversed pattern, with central buds opening before lateral buds (Singh *et al.*, 2011c; Singh *et al.*, 2014d).

Synchrony of Anthesis and Anther Dehiscence: Anther dehiscence occurred in precise synchrony with anthesis, with all anthers within a flower dehiscing simultaneously and releasing pollen in cohesive masses.

Mechanism of Anther Dehiscence: The dehiscence process involved longitudinal slits that initiated near the basal end of the anther lobe and extended toward the apex, facilitating efficient pollen release.

Pollen viability and stigma receptivity

Pollen Viability in Newly Opened Flowers: In all varieties of bael (*Aegle marmelos*), newly opened flowers exhibited high pollen viability, consistently exceeding 95%.

Stigmatic Receptivity and Anthesis: The stigma, initially non-receptive during the bud stage, became receptive immediately upon flower opening. Stigmatic receptivity coincided with anthesis and anther dehiscence and persisted for approximately 48 hours.

Variation in Stigma Receptivity Across Varieties: The highest stigma receptivity was recorded on the day of anthesis, ranging from 45.27% to 68.53% across all varieties. Among these, the maximum receptivity was observed in the Pant Urvashi variety, followed by Goma Yashi, with NB-7 showing the lowest values.

Temporal Dynamics of Stigma Receptivity: Receptivity was significantly lower on the day before anthesis (7.95% to 15.52%) and the day after (3.62% to 14.37%), highlighting the critical window for effective pollination during peak receptivity on the day of anthesis (Singh *et al.*, 2014a; Singh *et al.*, 2019b).

Inflorescence morphology

Floral morphology

Bisexual flowers in bael (*Aegle marmelos*) are borne in clusters, appearing as greenish-white axillary or terminal cymes.

Calyx Structure: The calyx is shallow and comprises 4 or 5 short sepals, which are either tetramerous or pentamerous, featuring broad teeth and a pubescent exterior.

Petal Characteristics: The petals are oblong-oval, typically numbering 4 or 5, with occasional occurrences of 6 or 7. They are pale greenish-white in color.

Stamen Features: The stamens are numerous and hypogynous, characterized by short filaments.

Variations in Floral Phenology: Key floral traits such as bud emergence, flowering duration, anthesis timing, anther dehiscence, stigma receptivity, and pollen viability exhibit significant variability across different varieties and locations (Singh *et al.*, 2011; Singh *et al.*, 2014a).

Evaluation of Floral Organ Dimensions:

The size and shape of floral organs, including bud size, flower size, and petal size, were assessed for multiple bael varieties under the rainfed conditions of the semi-arid ecosystem at CHES, Godhra (Singh *et al.*, 2016).

Variability in Floral Organ Dimensions: Significant variation was observed in the dimensions of floral organs across bael (*Aegle marmelos*) varieties. Measurements ranged as follows: bud length (10.00–13.5 mm), bud width (7.25–9.80 mm), flower length (12.25–19.5 mm), flower width (22.00–35.75 mm), pedicel length (4.25–10.75 mm), pedicel width (2.00–2.75 mm), petal length (11.50–19.25 mm), petal width (7.25–10.50 mm), stamen length (6.25–9.50 mm), filament length (2.75–5.50 mm), filament width (0.45–0.85 mm), anther length (3.25–4.75 mm), anther width (0.50–0.75 mm), pollen diameter (41.25–45.50 microns), ovary length (4.25–8.50 mm), ovary diameter (2.25–5.25 mm), style length (1.00–1.75 mm), style width (1.50–2.75 mm), stigma length (2.25–3.50 mm), and stigma width (2.25–3.00 mm).

Bud Dimensions: The maximum bud length and width were recorded in NB 17 and CISH-B 2, respectively. The shortest bud length was observed in Pant Aparna, followed by NB 9 and NB 16. The smallest bud width was found in CISH-B 1, followed by Pant Shivani and Pant Sujata (Singh *et al.*, 2014).

Flower Size: Flower size, measured in terms of length and width, was largest in CISH-B 2 and NB 7, respectively. The smallest flower dimensions were noted in Goma Yashi, followed by NB 9 and NB 16 (Singh *et al.*, 2014).

Pedicel Dimensions: Maximum pedicel length and width were observed in NB 5, followed by Pant Aparna and Pant Sujata. The shortest pedicel length and width were recorded in NB 9 and NB 16 under rainfed conditions (Singh *et al.*, 2014).

Petal Dimensions: The maximum petal length was found in NB 7, while the widest petals were observed in Pant Aparna. The shortest petal length and width were recorded in NB 9, followed by NB 16 and CISH-B 2 (Singh *et al.*, 2014).

Superior Floral Traits in NB-7: Overall, NB-7 exhibited larger floral organs compared to other varieties, suggesting its potential advantage in reproductive success.

Stability of Floral Traits: Floral traits, being among the most conserved characteristics, were minimally influenced by environmental factors, underscoring their reliability for

Variation in flower colour and size

Pollination

Pollination's Role in Fruit Set: The significance of pollination in fruit sets varies considerably among different cultivars and is influenced by factors such as the availability and quality of functional pollen, the characteristics of the pollen, the relationship between pollen availability and seed set, and the capacity of certain cultivars to produce parthenocarpy fruits, with or without pollination (Neeraj *et al.*, 2017).

Self-pollination and Cross-pollination in Bael: In *Aegle marmelos* (bael), approximately 5% of flowers undergo self-pollination, while 95% depend on insect-mediated cross-pollination. As a primarily cross-pollinated species, bael requires a compatible pollinizer variety to enhance the fruit set, which varies significantly among cultivars based on the quantity of functional pollen and its relationship with fruit setting (Singh *et al.*, 2014a, 2018b).

Clonal Variation in Flower Morphology: Singh *et al.* (2014a, 2018b) reported clonal variation in the morphology of bael flowers and inflorescences, indicating the impact of genetic differences on reproductive success. The fragrant flowers, typically arranged in clusters of 4 to 7 along young branchlets, feature 4 or 5 fleshy petals with a green exterior and yellowish interior, alongside 50 or more greenish-yellow stamens.

Pollinators in Bael's Flowering Period: During the flowering period (May-June), bael flowers attract a variety of insect pollinators, including honey bees (*Apis dorsata*, *Apis mellifera*), beetles, house flies, ants, and butterflies, which forage between 6 AM and 1 PM. These pollinators access the central portions of flowers, whether fully open or in the early stages of opening, and carry significant amounts of pollen on their bodies, primarily on their abdomens and legs (Singh *et al.*, 2019a).

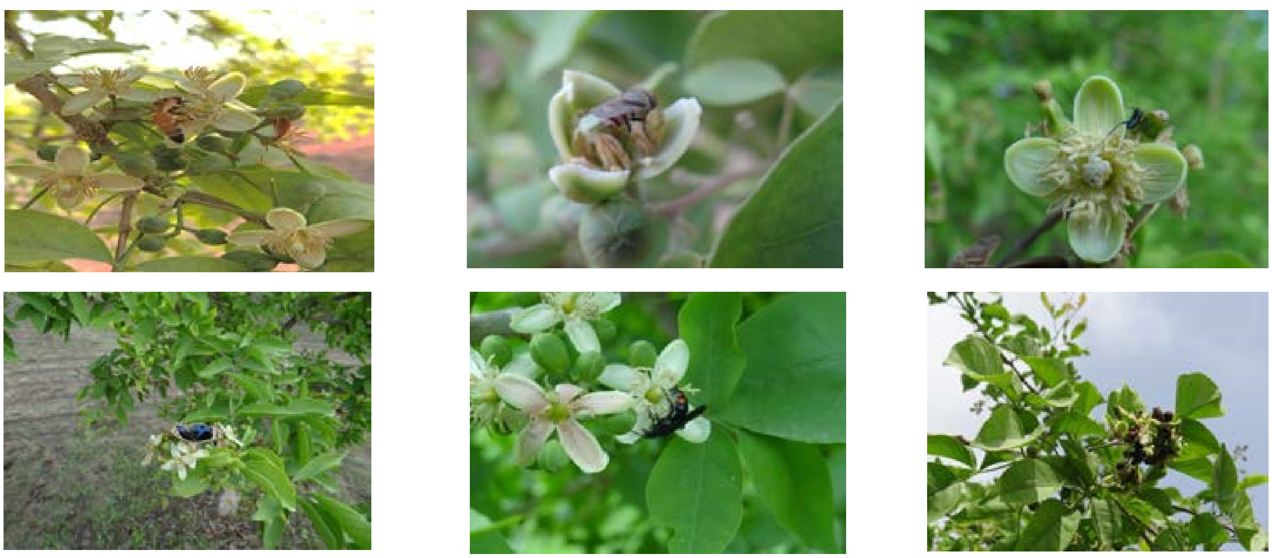
Monitoring Insect Activity for Pollination Study: Insect activity was monitored at one-hour intervals to study insect pollination. Honey bees were found to be the most effective pollinators, visiting each flower 5 to 23 times per hour and carrying an average of 29.65 pollen grains per visit, surpassing other pollinators in both frequency and pollen load (Singh *et al.*, 2014a).

Role of Honey Bees as Primary Pollinators: Honey bees have been established as the primary and most efficient pollinators for bael, contributing significantly to the reproductive success of the crop. Their foraging behavior and high pollen-carrying capacity make them the most legitimate pollinators for bael and many other tropical fruit trees (Singh *et al.*, 2019c, 2019b, 2021a).

Controlled Pollination and Pollination Methods: The pollination mechanism in *Aegle marmelos* (bael) was examined through controlled pollination experiments. Unopened flowers and panicles were bagged with butter paper bags to isolate them from external pollination. To assess the extent of self-pollination (autogamy), flowers were bagged before anthesis. Manual crosses were performed to investigate the occurrence of geitonogamy and xenogamy, while emasculated flower buds were bagged to explore the potential for apomixis. The fruits and seeds produced from these crosses were subsequently counted to evaluate reproductive success.

Bael as a Cauliflorous Fruit Tree: Bael is a prime example of a cauliflorous fruit tree, where flowers and fruit can emerge directly from the main trunk and old branches (Singh *et al.*, 2018b). This characteristic allows the tree to adapt to various environmental conditions. In bael, flowering and fruiting can occur not only on the current season's shoots but also on shoots up to 10 years old, including those on the main trunk, providing a unique reproductive advantage (Singh *et al.*, 2019f).

Metaxenia in Bael: The phenomenon of metaxenia, which refers to the direct influence of pollen grains on the external parts of the fruit (such as size and shape) outside the embryo and endosperm, was observed in bael. Metaxenia has been found to shorten the fruit development period and increase yield, especially in mixed cultivar plantings. A metaxenia effect, ranging from 2-5%, was observed in the fruit shape and ripening period across various genotypes of bael (Singh *et al.,* 2014, 2015, 2018).



Different pollinators in bael

Mechanism behind metaxenia

The most plausible explanation for metaxenia is the secretion of hormones or soluble substances by the embryo, endosperm, or both, which directly influence the external fruit characteristics. Although this phenomenon has been noted in bael, it has not been previously documented in detail. The pollen source plays a significant role in determining the size, shape, fruit set, stylar cavity, and fruit development rate in bael, thereby affecting the ripening time and quality of bael fruits (Singh *et al.*, 2018b, 2018a, 2019a, 2021a).

Conclusion

There are significant gaps in the available knowledge of pollination and pollinators in bael fruit tree. To bridge these gaps, it is essential to analyze and compare pollinator diversity and effectiveness across species, assessing their contributions to bael crop productivity and economic value. This review explores the diversity and efficiency of pollinator species, offering insights into their economic impact on bael cultivation. Insect pollination, particularly by bees, plays a crucial role in bael production, emphasizing the importance of conserving bee populations to enhance pollination and increase yields. Among all pollinators, the giant honeybee (*Apis dorsata*) stands out as the most effective and legitimate pollinator for bael, significantly improving fruit set and boosting overall yield. Further research is needed to elucidate the influence of pollinators on the internal and external physiological traits of bael fruits. Unfortunately, many fruit growers fail to recognize the importance of maintaining sufficient pollinizers and pollinators in their orchards due to a lack of awareness about their critical role in pollinating commercial varieties. Enhancing honeybee colony presence in cropping areas offers a practical solution, with the potential to substantially improve both the quality and quantity of bael fruits.

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Conflict of Interest

The authors have no conflict of interest.

Data Sharing

All relevant data are within the manuscript.

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