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FROM BLOOM TO BEAN: ADVANCES IN COCOA POLLINATION BIOLOGY, ECOLOGY AND SUSTAINABLE YIELD ENHANCEMENT

A.S. Vaishnavi[1], A. Aswini[2]*, Najitha Ummer[3], Deepu Mathew[4] and P. Anitha[1]

[1]Department of Plantation, Spices, Medicinal and Aromatic crops, College of agriculture, Vellanikkara, Kerala Agricultural University, Vellanikkara, Kerala, India.

[2]Department of Horticulture, Cocoa Research Centre, Kerala Agricultural University, Vellanikkara, Kerala, India.

[3]Department of Agricultural Entomology, Cocoa Research Centre, Kerala Agricultural University, Vellanikkara, Kerala, India.

[4]Centre for Plant Biotechnology and Molecular Biology, College of Agriculture, Vellanikkara, Kerala, India.

*Corresponding author E-mail : aswini.a@kau.in

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ABSTRACT

Cocoa (*Theobroma cacao* L.) is one of the world's most important plantation crops and the principal raw material for the global chocolate industry. Despite producing thousands of flowers annually, only a small proportion develop into mature pods, making pollination a major biological constraint to cocoa productivity. This review synthesizes recent advances in cocoa pollination biology, emphasizing the relationships among floral architecture, flowering ecology, pollinator diversity, and assisted pollination strategies. Cocoa possesses highly specialized flowers with petal hoods, fertile stamens, sterile staminodes, and a self-incompatibility system that collectively promote cross-pollination while restricting self-fertilization. Successful pollination depends predominantly on ceratopogonid midges, particularly *Forcipomyia* spp., whose abundance is strongly influenced by shade, temperature, rainfall, humidity, and the availability of decomposing organic substrates that serve as breeding habitats. The review highlights the influence of environmental and physiological factors regulating flowering phenology and examines how pollinator-friendly management practices, including shade regulation, mulching, organic matter conservation, and biodiversity enhancement, improve pollination efficiency and fruit set. Recent evidence demonstrates that assisted pollination significantly increases pod set and yield, often outperforming conventional nutrient and pesticide inputs, making it a valuable approach for commercial plantations and breeding programmes. Furthermore, advances in understanding self-incompatibility mechanisms have improved controlled hybridization and genetic improvement efforts. Integrating ecological pollinator conservation with assisted pollination technologies offers a sustainable pathway for reducing pollination deficits and enhancing cocoa productivity under changing climatic conditions. Future research should focus on developing mechanized pollination systems, conserving pollinator habitats, and integrating pollination management into climate-resilient cocoa production systems to ensure long-term productivity, farmer livelihoods, and global chocolate supply.

Key words : Cocoa (*Theobroma cacao* L.), Sustainable yield, Pollination systems, Pollinator diversity.

Introduction

Cocoa (*Theobroma cacao* L.) is the world's third most important beverage crop after coffee and tea and is one of the most valuable commercial plantation crops cultivated in the humid tropics. It is the principal raw material for the global chocolate industry, which generates billions of dollars annually and provides income and livelihood opportunities for more than 50 million people, including approximately 5–6 million smallholder farming households across tropical regions (ICCO, 2025). Beyond its economic value, cocoa contributes significantly to rural development, employment generation, biodiversity conservation through agroforestry systems and the socio-economic sustainability of many developing countries (Tscharntke *et al.*, 2011; Schroth and Harvey, 2007).

Globally, cocoa is cultivated on more than 11 million hectares with an annual production of approximately 5 million tonnes. However, despite its extensive cultivation,

average productivity remains relatively low, indicating a substantial gap between the crop's genetic yield potential and actual field performance (ICCO, 2025). This low productivity reflects the crop's dependence on favourable environmental conditions, the predominance of low-input smallholder production systems, and its susceptibility to numerous biotic and abiotic constraints (Läderach *et al*., 2013). Among cocoa-producing countries, Ghana occupies a pivotal position in the global cocoa market as one of the world's leading producers and exporters of premium-quality cocoa beans. The cocoa sector is the country's most important agricultural export industry, contributing significantly to foreign exchange earnings, national economic growth and the livelihoods of more than 800,000 smallholder farming households (Anim-Kwapong and Frimpong, 2004; Kolavalli and Vigneri, 2011; Vigneri and Kolavalli, 2018). Owing to its strategic role in supplying high-quality cocoa beans to the international chocolate industry, improving cocoa productivity in Ghana is essential not only for enhancing farmer livelihoods and the national economy but also for ensuring the stability and sustainability of the global cocoa supply chain (Wanger *et al.*, 2021; ICCO, 2025).

Several factors contribute to the persistent yield gap in cocoa production, including aging plantations, inferior planting materials, declining soil fertility, inadequate crop management practices, insect pests such as tea mosquito bug and stem borer, devastating diseases such as black pod and vascular streak dieback, and the increasing impacts of climate change (Schroth *et al*., 2016). Among these constraints, inadequate pollination remains one of the most critical, but frequently overlooked limitations to cocoa productivity (Young, 1986; Groeneveld *et al*., 2010). Cocoa exhibits a unique reproductive biology characterized by prolific flowering, with a mature tree producing several thousand flowers annually. Nevertheless, only a very small proportion of these flowers successfully develop into mature pods. Natural pollination rates are generally less than 10%, while fruit set commonly ranges from below 5% to about 40%, with a large proportion of developing fruits aborted during early developmental stages (De Almeida and Valle, 2007). Effective pollination depends primarily on tiny ceratopogonid midges (*Forcipomyia* spp. and *Dasyhelea* spp.), whose abundance is strongly influenced by plantation microclimate, shade management, organic matter availability, and suitable breeding substrates (Kaufmann, 1975; Winder, 1978; Toledo-Hernández *et al*., 2021).

Given the ecological dependence of cocoa on specialized insect pollinators, improving pollination efficiency has emerged as a sustainable and environmentally sound strategy for enhancing cocoa productivity. Management practices such as conserving shade trees, maintaining leaf litter and decomposing organic substrates, providing suitable breeding habitats for pollinating midges and supplementing natural pollination through assisted pollination can substantially increase fruit set and yield while simultaneously promoting biodiversity and ecosystem resilience (Toledo-Hernández *et al*., 2021; Vansynghel *et al*., 2022; Jaramillo *et al*., 2024). Therefore, strengthening pollination ecology represents a promising approach for sustainable cocoa production and should be considered an integral component of future cocoa improvement and plantation management programmes

Floral biology of cocoa and it's unique floral architecture

Cocoa flowers (*Theobroma cacao*) are small, about 15 mm in diameter and grow directly on the stems and branches of the tree forming cauline inflorescences, a unique growth habit known as cauliflory or truncation. This adaptation allows the tree to produce a high density of flowers in a compact space, optimizing pollination efficiency. Flowers are produced only on wood that has attained a minimum physiological age of about two to three years under favourable growing conditions. The floral formula of cocoa is $K_5\ C_5\ A_5+_5\ G(5)$ and the flowers are hermaphroditic and pentamerous, meaning they possess five whorls of floral organs: sepals, petals, stamens, staminodes, and carpels. The five sepals are white and sparsely pubescent on the abaxial side, remaining free from one another. The five petals are pale yellow, free, and distinctly shaped which is narrow at the base, expanding into a cup-shaped pouch, and ending in a broad tip or ligule (Bartley, 2005). The petals are cucullate in the middle and pedicellate at the base, forming hoods that house the anthers of the stamens. The androecium consists of ten stamens arranged in two whorls: the inner whorl has five fertile stamens bearing two anthers each, while the outer whorl has five long, non-fertile staminodes. The staminodes are purple and are located between the stamens and the carpels, enhancing the flower's intricate morphology (Jaramillo *et al*., 2024). The ovary of the cocoa flower is superior and contains between 40 and 70 ovules, which, upon successful fertilisation, develop into the seeds within the cocoa pod. The surface of the petal hoods bears longitudinal guiding lines that help direct pollinators to the reproductive structures (Amma *et al*., 2012). The ovary has 40–70 ovules, imparting a lot of reproductive potential under favourable pollination (Wood and Lass, 2001).



Fig. 1 : Cocoa flowers.

The floral architecture of cocoa (*Theobroma cacao* L.) exhibits a highly specialized structural organization that promotes precise pollen transfer and enhances reproductive efficiency. The coordinated arrangement of the floral hood, fertile stamens, sterile staminodes and stigma forms a sophisticated pollination mechanism that restricts pollen loss, regulates pollinator access, and favours cross-pollination. The intricate spatial relationship among these floral organs ensures that only appropriately sized pollinators can access the reproductive structures, thereby improving pollination success (Amma *et al*., 2012; Jaramillo *et al*., 2024).

A distinguishing feature of cocoa flowers is the unique morphology of the petals. Each of the five petals is bilobed, comprising a narrow basal ligule and an upper cucullate (hood-shaped) lobe that forms the characteristic floral hood . The ligule extends outward and often curves inward towards the floral centre, creating narrow channels that guide visiting insects towards the reproductive organs. The hood encloses the anther of a fertile stamen, protecting pollen from rainfall, desiccation and accidental loss while simultaneously acting as a selective barrier that permits entry only to small pollinating insects. The inner surface of the hood contains microscopic nectaries and longitudinal guiding lines that secrete minute quantities of nectar and provide tactile and visual cues to pollinators. Following anther dehiscence, pollen grains accumulate within the hood, forming a secondary pollen presentation site where pollen remains protected until removed by visiting insects. This specialized arrangement minimizes pollen wastage and increases the efficiency of pollen transfer by forcing pollinators to crawl through the narrow hood entrance, thereby contacting both pollen and the reproductive organs (Amma *et al*., 2012).

The androecium of cocoa consists of ten stamens arranged in two alternating whorls, of which only five are fertile while the remaining five are sterile staminodes. Each fertile stamen is positioned beneath a petal hood, and its recurved filament elevates the anther into the hood chamber, ensuring that pollen is released within this enclosed structure rather than directly into the environment. During the male phase of anthesis, the anthers dehisce and release sticky pollen grains into the hood cavity, where they remain viable for approximately 24 hours (Jaramillo *et al*., 2024). Because cocoa pollen is heavy and adhesive, it is not adapted for wind dispersal and depends entirely on mechanical transfer by insects, particularly ceratopogonid midges (Toledo-Hernández *et al*., 2021). The close association of the fertile stamens with the floral hood also creates a humid microenvironment that helps preserve pollen viability while functioning as a selective filter that restricts access to pollinators capable of navigating the narrow floral passages.



(a) **(b)** **(c)**

Fig. 2 : Unique floral architecture of cocoa (a) Floral hood , (b) Stamens and their positioning, (c) Staminode–Stigma Interaction.

The five sterile staminodes play a crucial role in regulating pollination by controlling access to the stigma. These petaloid, purple-coloured structures are positioned alternately between the fertile stamens and the central gynoecium and terminate near the upper region of the ovary. During the male phase of anthesis, the staminodes curve inward and partially enclose the stigma, thereby reducing the likelihood of self-pollination. After pollen dehiscence is completed, the staminodes gradually recurve outward, exposing the five-lobed stigma during the female receptive phase. At this stage, the stigma becomes glistening and sticky, facilitating the reception of pollen carried by pollinating insects. Thus, the sequential movement of the staminodes acts as a functional gating mechanism that synchronizes pollen release with stigma receptivity and promotes outcrossing.

Based on the relative position of the staminodes to the style, cocoa flowers have been classified into three morphological types: converging,parallel, and splay. In the converging type, the staminodes bend inward and nearly meet around the style column, partially enclosing the stigma. In the parallel type, the staminodes remain upright and aligned alongside the style without substantial inward curvature, whereas in the splay type they spread outward from the style, leaving the stigma relatively exposed. Evaluation of staminode-style distance in relation to fruit set revealed that converging flowers constituted the majority (56.0%) of the population, followed by parallel (37.5%) and splay (6.5%) types. Flowers with parallel

staminodes recorded the highest fruit set (15.6%), although it was not significantly different from that of converging flowers (11.8%). In contrast, flowers possessing splay staminodes exhibited a significantly lower fruit set (0.5%), indicating that staminode orientation strongly influences pollination efficiency and reproductive success (Frimpong-Anin *et al*., 2014). These findings suggest that the spatial arrangement of the staminodes relative to the stigma is an important floral trait affecting fertilization and subsequent pod development in cocoa.

Floral anthesis

Cocoa flowers are protandrous and predominantly exhibit nocturnal anthesis, which can be characterized into four distinct developmental stages. The first stage which last for approximately 14 hours, involves floral opening initiated by the outward pressure of expanding petals causing the sepals to separate. At this point, floral structures are pale, and trichomes appear translucent, except for the distinctly red staminodes. The second stage corresponds to the male phase. During this period, the anthers dehisce, releasing pollen grains, while the staminodes remain closed, covering the still-closed stigma. The third stage marks the female phase where staminodes open and expose receptive stigma. Floral structures at this point exhibit noticeable darkening, ovaries turn reddish-purple, trichomes become deep red, and staminodes appear glossy. The duration of the female phase varies with the flower's position on the floral cushion lasting approximately 24 hours for most flowers, but extending up to 48 hours for those located centrally. The final stage involves floral senescence , characterized by browning of all floral organs except the ovary. The complete lifespan of a cocoa flower ranges from 72 to 78 hours (Jaramillo *et al*., 2024). But in Indian condition, anthesis starts in late afternoon (14.00 and 16.00 hrs) and are fully opened by the forenoon of the next day (02.00 and 04.00hrs). Anther dehiscence starts between 04.00 and 05.00 hrs and is completed between 08.00 and 10.00 hrs. Stigma becomes receptive on the second day of the anthesis and it may reduce after 10.00 hrs (Amma *et al*., 2012).

Ecology of flowering

Flowering in cocoa (*Theobroma cacao* L.) is regulated by a complex interaction of environmental (exogenous) and physiological (endogenous) factors that determine the timing, intensity, and periodicity of flowering. Among the environmental factors, rainfall is the primary driver of flowering phenology, with flowering being suppressed during prolonged dry periods and stimulated following the onset of rainfall (Adjaloo *et al*., 2012). Temperature and solar radiation further influence flower initiation and fruit set, while regions with uniformly distributed rainfall and stable temperatures support year-round flowering. Nevertheless, cocoa trees exhibit rhythmic alternation between vegetative and reproductive growth, resulting in irregular bearing patterns that often coincide with seasonal rainfall cycles, such as the major and minor crop seasons observed in Côte d'Ivoire (Wibaux *et al*., 2024).

In addition to climatic influences, cocoa flowering is regulated by intrinsic physiological and genetic mechanisms. Flowering follows a genetically controlled rhythm that persists even under relatively constant environmental conditions. Fruit load suppresses subsequent flowering, contributing to alternate bearing, while vegetative growth processes, including leaf flushing, root development, and cambial activity, compete for assimilates and further influence reproductive activity. Endogenous factors such as carbohydrate reserves, carbon-to-nitrogen ratio and hormonal balance also regulate floral initiation and intensity. Influence of auxin, cytokinin and gibberellic acid which manage the transition from vegetative buds to reproductive flower cushions and also promotes the percentage of fertilization in cocoa flowers (Tanny *et al*., 2023). Furthermore, considerable genotypic variation exists in flowering behaviour, with different cocoa genotypes exhibiting distinct flowering rhythms and seasonal responses (Minimol *et al*., 2020). Therefore, cocoa flowering represents the outcome of a dynamic interaction between climatic factors, particularly rainfall, temperature, seasonality and internal physiological and genetic controls, all of which are critical for optimizing productivity.

a) **Rainfall :** Rainfall is the most important environmental factor regulating cocoa flowering and productivity. Cocoa thrives in humid tropical regions with well-distributed rainfall, and optimum flower production occurs when rainfall exceeds 150 mm, which ensures adequate soil moisture for leaf flushing, floral initiation, and fruit development . Water stress caused by prolonged dry periods suppresses flower initiation, increases flower abortion, and may lead to wilting of floral buds and immature pods. Conversely, the onset of rainfall after drought triggers synchronized flowering by restoring metabolic and hormonal activities and improving nutrient uptake and carbohydrate translocation required for floral bud differentiation (Adjaloo *et al*., 2012).

b) **Temperature :** Temperature is another key determinant of cocoa flowering, although its influence is secondary to rainfall. The optimum temperature

for floral initiation and flowering ranges from 18–23°C, with maximum flower production reported at 22–23°C (Adjaloo *et al*., 2012). Temperatures above 23°C reduce flowering by increasing transpiration, water stress, and disrupting hormonal regulation, whereas temperatures below 18°C slow floral bud initiation. Under Indian conditions, cocoa is cultivated mainly as an intercrop in Kerala, Karnataka, Tamil Nadu and Andhra Pradesh, where temperatures generally range from 20–32°C. Flowering is most prolific during the cooler months (November–February), while summer temperatures (>30°C) suppress flower production. The flowering period varies with respect to the geographic location where in Kerala profuse flowering occurs during post monsoon and last till late January and in Andhra Pradesh flowering occurs peak during September-October (Janaki *et al*., 2018). Therefore, adequate shade and irrigation are essential to moderate temperature stress and sustain flowering (Amma *et al*., 2012).

c) Seasonal influence : Seasonal variation strongly influences cocoa flowering. In Ghana, flowering follows a segmental pattern with peak floral production during the major rainy season (April–July) and a marked decline during the minor rainy season (September–November). In Ghana, cocoa exhibits a segmental flowering pattern with repeated flowering phases throughout the year, largely influenced by seasonal rainfall. Flowering is most abundant during the major rainy season (April–July), peaking in July, with flowers produced on the trunk, branches, and canopy. Flowering declines during the minor rainy season (September–November) and becomes sparse during the dry season (December–March). Cherelle production is highest from June to August, while fruit set gradually increases from April and reaches its peak in September, reflecting the positive influence of rainfall on reproductive development (Adjaloo *et al*., 2012). Similar trends have been reported in India, where flowering is highest during the monsoon or post-monsoon season depending on genotype and is substantially reduced during summer because of high temperature and moisture stress (Minimol *et al*., 2020). These seasonal differences highlight the combined influence of environmental conditions and genotypic variability on flowering phenology, emphasizing the importance of genotype-specific management for improved productivity.

d) Mulching : Mulching plays an important role in enhancing cocoa flowering by conserving soil moisture, moderating soil temperature, improving soil fertility through organic matter decomposition, and reducing weed competition. These effects help maintain continuous vegetative growth and support floral initiation, particularly during dry periods when water stress can limit flowering. Organic mulches such as cocoa pod husks, leaf litter, and other plant residues gradually release nutrients, improve soil structure and promote microbial activity, creating favorable conditions for flower and pod development (Anim-Kwapong and Frimpong, 2004). In addition, adequate soil moisture maintained by mulching reduces physiological stress, thereby increasing flower production and improving fruit set (Carr and Lockwood, 2011). Application of cocoa husks as mulch has been reported to enhance flower production, indicating its potential to improve pollination and overall cocoa yield by conserving soil moisture and creating favourable microclimatic conditions (Forbes and Northfield, 2017).

Pollination Mechanism in Cocoa

Cocoa (*Theobroma cacao* L.) is predominantly a cross-pollinated species owing to a combination of specialized floral adaptations and genetic self-incompatibility mechanisms that restrict self-fertilization and promote outcrossing. The flower possesses a complex floral architecture in which the petal hoods partially enclose the reproductive organs, while sticky pollen grains facilitate adherence to insect pollinators rather than direct deposition on the stigma. Sterile staminodes positioned between the fertile stamens and the gynoecium act as physical barriers that limit self-pollen deposition and regulate access to the stigma (Young, 2007). In addition, cocoa exhibits a gametophytic self-incompatibility system that prevents fertilization by self or genetically related pollen, thereby ensuring successful fertilization primarily through genetically distinct pollen (Ríos-Moyano *et al*., 2025). Consequently, the small flower size, specialized floral architecture, sticky pollen, and self-incompatibility make cocoa highly dependent on insect pollinators, particularly ceratopogonid midges, for effective pollination, fruit set, and the maintenance of genetic diversity and crop productivity (Toledo-Hernández *et al*., 2021).

Self-incompatibility in Cocoa

Self-incompatibility (SI) in cocoa (*Theobroma cacao* L.) is a genetically controlled reproductive mechanism that prevents self-fertilization and promotes outcrossing, thereby maintaining genetic diversity. The SI system is governed by the multiallelic S locus, comprising five alleles (S_1 –S_5) that exhibit a hierarchical dominance relationship



Fig. 3 : Strategies developed to overcome self-incompatibility a) bud pollination, b) intra-ovarian pollination and c)surgical pollination (Narayanapur, 2019).

($S_1 > S_2 = S_3 > S_4 > S_5$). Each genotype possesses two S alleles that function independently as male and female determinants. During pollination, pollen tube growth is arrested when the male determinant of the pollen matches either of the female determinants expressed in the pistil, resulting in incompatibility. These allelic combinations, referred to as S haplotypes, determine the compatibility relationships among cocoa genotypes (Narayanpur, 2019).

Although, SI acts as a natural barrier to self-fertilization, it plays a dual role in cocoa improvement. By enforcing cross-pollination, it enhances genetic diversity and facilitates the production of vigorous hybrid progenies with superior yield, adaptability and disease resistance. Conversely, SI restricts the development of homozygous inbred lines, posing a major challenge for genetic studies and breeding programmes. To overcome this limitation, several artificial pollination techniques have been developed, including bud pollination, surgical pollination, and intra-ovarian pollination as shown in Fig. 2. Bud pollination involves pollinating immature flower buds before stigma receptivity, surgical pollination places pollen on a partially excised style after removal of the stigmatic surface, and intra-ovarian pollination bypasses the stigma by directly depositing pollen onto the ovary after style excision. Using these approaches, the Cocoa Research Centre (CRC), Kerala Agricultural University, has successfully developed cocoa inbred lines up to the sixth generation, representing a significant milestone in cocoa breeding and facilitating the development of genetically uniform lines for advanced breeding and genetic research (Narayanpur, 2019).

Assisted pollination in cocoa

Assisted pollination is an important agronomic and breeding intervention in cocoa (*Theobroma cacao* L.) involving the manual transfer of pollen from the anther to the receptive stigma. Natural fruit set in cocoa is generally low due to its complex floral architecture, self-incompatibility, and insufficient pollination by natural insect vectors, particularly ceratopogonid midges (Toledo-Hernández *et al*., 2017; Forbes *et al*., 2019; Lander *et al*., 2025). Consequently, assisted pollination enhances pollen deposition, fertilization, pod set, and overall yield, while serving as an essential tool for controlled hybridization and seed production in breeding programmes (Toledo-Hernández *et al*., 2017; Toledo-Hernández *et al*., 2020).

For controlled hybridization, flower buds expected to open on the following day are enclosed to prevent insect visitation. At anthesis, pollen from freshly opened flowers of the selected male parent is transferred onto the receptive stigma of the female flower. Owing to cocoa's self-incompatibility system, emasculation is generally unnecessary except during selfing. Pollinated flowers are tagged, and successful fertilization is confirmed by ovary enlargement within 3–5 days (Amma *et al*., 2012; Narayanpur, 2019). In commercial plantations, particularly polyclonal orchards, a simplified form of assisted pollination can be practiced by transferring pollen between freshly opened flowers of genetically distinct trees. This inexpensive technique promotes cross-pollination, exploits cocoa's self-incompatibility system, and improves pod set without requiring specialized equipment (Amma *et al*., 2012).

Recent studies have demonstrated the substantial benefits of assisted pollination. A comprehensive review by Toledo-Hernández *et al*. (2017) concluded that pollination is one of the major factors limiting cocoa productivity and emphasized the potential of enhanced pollination services to close yield gaps. Experimental studies further showed that even partial hand pollination significantly increased cocoa yield and farmer income, outperforming conventional fertilizer and pesticide inputs (Toledo-Hernández *et al*., 2020). In addition, supplemental and synchronized pollination has been reported to improve fruit set and yield under commercial production systems (Forbes *et al*., 2019). A global analysis across Brazil, Ghana, and Indonesia demonstrated that hand pollination increased cocoa yield by approximately 20%, confirming that pollination limitation, rather than nutrient limitation, is a primary constraint to cocoa production (Lander *et al*., 2025). Hand pollination has been shown to markedly improve cocoa productivity, with studies reporting increases in fruit set ranging from 250% to 1631% and mature fruit production from 86% to 775% compared with natural pollination (Toledo-Hernández *et al*., 2020; Vansynghel *et al*., 2022a). Furthermore, adoption of hand pollination improved cocoa tree productivity by 15.3% among smallholder farmers in Ghana (Wongnaa *et al*., 2021). Furthermore, assisted pollination was found to be most effective under low to

moderate canopy cover, where increased pollinator activity and reduced shading enhanced fruit set (Toledo-Hernández *et al*., 2023).

Natural pollination in cocoa

Natural pollination is a critical yet inherently inefficient process in cocoa (*Theobroma cacao* L.), representing one of the major biological constraints limiting fruit set and global cocoa productivity. Although, cocoa trees produce thousands of flowers annually, only about 0.5–5% of flowers develop into mature pods under natural conditions due to poor pollination efficiency and high rates of flower and cherelle abortion (Groeneveld *et al*., 2010). Cocoa pollination primarily depends on tiny dipteran insects, particularly ceratopogonid midges (*Forcipomyia* spp. and *Dasyhelea* spp.), which transfer pollen from the anthers to the receptive stigma during flower visits (Amma *et al*., 2012). The intricate floral architecture of cocoa, including the enclosed anthers within petal hoods, narrow access to nectar, and spatial separation of reproductive organs, restricts pollen transfer and makes successful natural pollination highly dependent on specialized pollinators (Jaramillo *et al*., 2024). Pollination success is strongly influenced by environmental factors such as temperature, rainfall, relative humidity, shade intensity, and the availability of suitable breeding habitats for pollinators, including decomposing leaf litter, cocoa husks, and decaying plant material (Toledo-Hernández *et al*., 2020; Vansynghel *et al*., 2022). Habitat degradation, excessive pesticide use, and climate variability can reduce pollinator abundance and activity, thereby lowering fruit set and pod yield (Toledo-Hernández *et al*., 2020). Studies have shown that effective fertilization requires the deposition of approximately 35–100 viable pollen grains on a receptive stigma, whereas an individual midge typically carries only around 20–30 pollen grains, necessitating multiple pollinator visits (approximately 4–8 visits) to achieve successful fertilization (Falque *et al*., 1995; Young, 1986). Despite its low efficiency, natural pollination remains indispensable for maintaining genetic diversity, ecosystem resilience and sustainable cocoa production without additional labour inputs. Consequently, promoting pollinator-friendly agroforestry systems, conserving organic breeding substrates, and minimizing indiscriminate pesticide application are considered essential strategies for enhancing natural pollination services and improving cocoa productivity (Toledo-Hernández *et al*., 2020).

Cocoa pollinator

The principal natural pollinators of cocoa worldwide are tiny flies from the family Ceratopogonidae, commonly

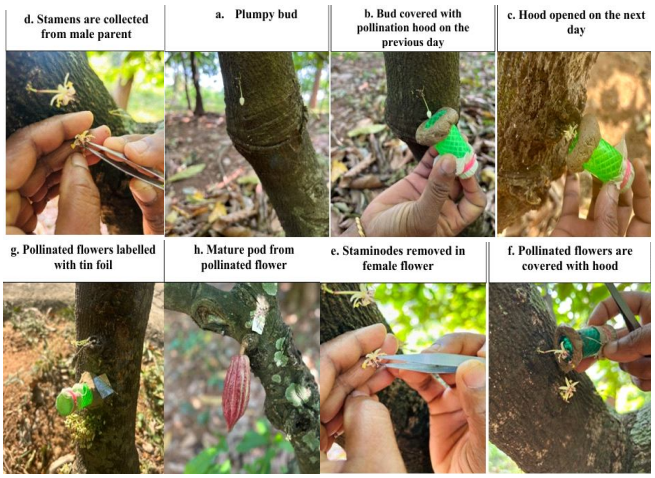


Fig. 4 : Hand Pollination in Cocoa.

known as biting midges or chocolate midges. These insects are extraordinarily small, measuring only 1-3 millimeters in length which allows them to navigate the intricate floral structures that exclude larger insects like honeybees.

Research in Ghana identified eight Ceratopogonidae species as effective cocoa pollinators, including four *Forcipomyia* species, two *Stilobezzia* species and one species each of *Culicoides* and *Atrichopogon*. Among these, *Forcipomyia* species, particularly *F. hardyi*, are recognized as the most important pollinators globally. Studies in Ghana documented that these midges contributed to an average of 27% of effectively pollinated flowers, though this varied widely from 6.5% to 60% depending on condition. Only female midges function as pollinators, attracted to cocoa flowers by a unique bouquet of floral volatiles composed exclusively of saturated and unsaturated straight-chain hydrocarbons, including tridecane, pentadecane, (Z)-7-pentadecene and (Z)-8-heptadecene. The sticky cocoa pollen adheres to the midge's hairy thorax as it navigates through the flower seeking nectar (Toledo-Hernández *et al*., 2017).

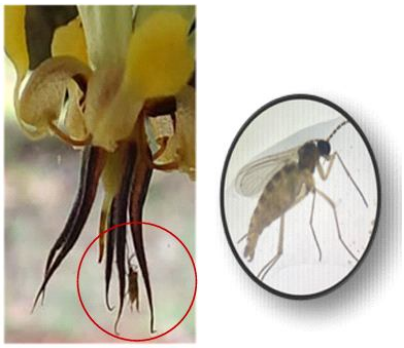


Fig. 5 : Pollinator in cocoa.

Cocoa pollination is primarily mediated by tiny ceratopogonid midges, particularly *Forcipomyia* spp., which are regarded as the most effective natural

pollinators of cocoa. Although a wide range of insects, including ants (*Camponotus acvapimensis*, *Crematogaster* spp., *Pheidole megacephala*), stingless bees (*Hypotrigona araujoi*) and gall midges (Cecidomyiidae), frequently visit cocoa flowers, only *Forcipomyia* spp. consistently achieve effective pollen transfer. While, Cecidomyiidae may exhibit relatively high visitation frequencies, *Forcipomyia* spp. deposit the greatest number of pollen grains on receptive stigmas (approximately 60 pollen grains per visit), making them the principal contributors to successful fertilization and fruit set (Adjaloo *et al*., 2013).

The remarkable pollination efficiency of *Forcipomyia* spp. is attributed to their minute body size and specialized foraging behaviour, which enables them to navigate the intricate floral architecture of cocoa. The midge initially lands on the staminodes and moves towards the petal hood in search of nectar, guided by floral guide lines. During this movement, its thorax brushes against the concealed anthers, allowing pollen grains to adhere to the body bristles. Upon visiting another flower, the adhered pollen is transferred to the style and subsequently reaches the receptive stigma. This indirect mechanism of pollen transfer has been reported to result in higher fruit set than direct pollen deposition (Kaufmann, 1975).

Recent studies continue to confirm the dominance of ceratopogonid midges in cocoa pollination. A survey conducted in Ecuador using yellow sticky traps identified five major ceratopogonid species associated with cocoa plantations: *Forcipomyia quatei*, *Forcipomyia youngi*, *Dasyhelea cacaoi*, *Dasyhelea borgmeieri* and *Culicoides pusillus*. Among these, *Forcipomyia* and Dasyhelea were the predominant genera and are well recognized as the principal cocoa pollinators (Montero-Cedeño *et al*., 2022). Similarly, a field study in Colombia reported that Diptera constituted 88.44% of all flower visitors, with Ceratopogonidae being the dominant family. Among the ceratopogonids collected, *Forcipomyia* sp., including *F. genualis*, were the most abundant taxa, further emphasizing their ecological importance in cocoa pollination (Ríos-Moyano *et al*., 2025).

However, the composition of flower-visiting insects can vary across geographical regions and production systems. In Indonesian cocoa agroforests, ants and other dipterans were the most abundant flower visitors, whereas ceratopogonid midges were not captured during sampling, despite being widely recognized as the primary cocoa pollinators in other studies. This finding suggests that pollinator communities are influenced by local environmental conditions, habitat characteristics, and sampling methods (Toledo-Hernández *et al*., 2020).

Ecology of pollinators

The ecology of cocoa pollinators is governed by a complex interplay of environmental, biological, and landscape factors that collectively influence their abundance, diversity, and pollination efficiency. Factors such as activity period, breeding substrate availability, shade level, forest connectivity, temperature, humidity, rainfall, and floral volatiles interact to determine the conditions that optimize pollination and enhance cocoa productivity. Moderate to dense canopy shade (40–70%) creates cool, humid microclimates that support midge survival and cocoa flowering, while proximity to natural or secondary forests provides breeding substrates and refuges that enhance pollinator abundance and movement. Optimal activity occurs at 22–28°C and high humidity (>75%), with extremes of temperature or moisture stress reducing efficiency and regular moderate rainfall maintaining suitable microhabitats for reproduction. Cocoa flowers emit faint volatile compounds during anthesis, aligning scent release with peak pollinator activity to optimize pollination and fruit set. Among which activity period and substrate plays a vital role (Montero-Cedeño *et al*., 2022).

The activity of cocoa pollinators, particularly Forcipomyia midges, follows a distinct diurnal pattern that is closely synchronized with cocoa flower receptivity. Midge activity begins shortly after sunrise, increases rapidly during the early morning, and reaches its highest level between 08:00 and 11:00 h. Thereafter, pollinator abundance gradually declines throughout the afternoon and becomes negligible by evening. This concentration of activity during the morning coincides with the period of maximum stigma receptivity, making it the most effective time for natural pollination and successful fertilization of cocoa flowers (Frimpong *et al*., 2009).

According to Adjaloo *et al*. (2013), the availability of organic mulch materials in cocoa plantations enhances the habitat and breeding sites of pollinating midges, resulting in improved pollinator abundance and increased cherelle production. Organic substrates such as banana pseudostem, cocoa pod husks , cocoa leaf litter provide favorable conditions for midge development promote natural pollination and reproductive success in cocoa. Among which banana pseudostem provided most suitable habit supporting highest midge population. Therefore, the incorporation of decomposing organic matter as mulch can serve as an effective ecological strategy to improve pollination efficiency and enhance cocoa productivity.

Substrate availability plays a pivotal role in sustaining

cocoa pollinator populations by providing suitable breeding and larval development sites for ceratopogonid midges. Organic substrates rich in moisture and decomposing plant material create favourable microhabitats that enhance pollinator abundance, thereby improving natural pollination and fruit set. In a study evaluating the effects of different breeding substrates, namely cocoa husks, leaf litter and banana pseudostems, banana pseudostems produced the highest fruit set under natural pollination (approximately 12%), owing to their high moisture content and decomposing organic matter, which provide ideal conditions for midge larval development. Under assisted pollination, leaf litter recorded the highest fruit set (approximately 20%), indicating that although manual pollination can compensate for pollinator limitation, substrate quality continues to influence reproductive success (Montero-Cedeño *et al*., 2022).

The importance of pollinator breeding substrates has also been demonstrated under field conditions. In North Queensland, Australia, the application of cocoa pod husks beneath the tree canopy significantly enhanced midge breeding, resulting in a 110-fold increase in cherelle production and a 60-fold increase in fresh fruit yield compared with untreated trees. As cocoa-pollinating midges are capable of dispersing beyond the canopy of individual trees, the benefits of substrate application extended to neighbouring trees, thereby improving pollination across a wider area (Forbes and Northfield, 2017). Similarly, the application of rotting banana pseudostems as a pollinator breeding substrate significantly increased cherelle production by creating a favourable habitat for cocoa pollinators. The positive effect was spatially dependent, with trees located within 1 m of the substrate producing significantly more cherelles than those situated farther away, indicating that the enhancement of pollinator activity and pollination success is greatest in the immediate vicinity of suitable breeding substrates (Vanhove *et al*., 2020). Collectively, these findings demonstrate that conserving and strategically introducing organic breeding substrates within cocoa plantations can enhance pollinator populations, improve natural pollination efficiency, and ultimately increase cocoa productivity.

Comparison of natural and assisted pollination in cocoa

Assisted pollination in cocoa markedly outperforms natural pollination in terms of fruit set and overall reproductive efficiency. In a comparative study, natural pollination of 1,952 cocoa flowers resulted in only 39 pods, corresponding to a fruit set rate of 2%, whereas assisted pollination of 968 flowers yielded 70 pods, or a 7% fruit set rate. This demonstrates that assisted pollination can enhance fruit set by approximately 3.5 times compared to natural pollination. These findings as shown in figure 13 strongly indicate that assisted pollination significantly improves reproductive success and yield outcomes in cocoa cultivation, providing a clear yield advantage over relying solely on natural pollinators (Vansynghel *et al*., 2022). Two pollination methods, natural and assisted manual, along with a control, were compared in an experiment where assisted pollination greatly outperformed natural pollination. The percentage of pollinated flowers was 20 compared to 9 under natural conditions, fertilized flowers were 16 compared to 4, and fruits formed were 15 compared to 4. These findings are consistent with previous studies reporting that manual pollination increases fruit set up to 25 percent or more, while natural pollination remains below 5 percent (Montero-Cedeño *et al.*, 2022).

Conclusion

Optimising cocoa yield necessitates enhancing pollination efficiency through both ecological and technological interventions. Conservation of key entomophilous pollinators, particularly ceratopogonid midges, which are the primary natural agents of cocoa pollination, plays a vital role in maintaining the reproductive success of the crop by ensuring favourable habitats that enhance their abundance and activity. Proper shade management maintains a cool, humid microclimate that prevents the breeding substrates from drying out and supports midge survival and activity. Maintaining adequate soil moisture through mulching and irrigation further creates suitable conditions for the development of immature stages of midges. The addition of decomposing organic materials, such as cocoa leaf litter, cocoa pod husks, banana pseudostems and other plant residues, provides ideal breeding and feeding substrates for pollinators by supplying moist, organic-rich habitats. Furthermore, minimizing the indiscriminate use of broad-spectrum insecticides and conserving on-farm biodiversity help protect pollinator populations and ensure their continuous activity. Collectively, these habitat management practices enhance pollinator abundance, improve pollen transfer, increase fruit set and ultimately contribute to higher cocoa productivity.

In addition to enhancing natural pollination, assisted pollination has emerged as an effective strategy for overcoming pollination limitations in cocoa. Among the available approaches, manual hand pollination is the most reliable and widely adopted method, particularly in

breeding programmes, seed gardens and plantations experiencing pollination deficits. Hand pollination ensures the precise transfer of viable pollen to receptive stigmas, thereby increasing fertilization success, fruit set and pod retention while reducing losses due to inadequate natural pollination. Despite these benefits, large-scale adoption of hand pollination is constrained by its high labour requirement, cost and the short duration of flower receptivity. Therefore, future research should focus on developing efficient mechanised assisted pollination technologies that can complement natural pollination and enable large-scale, cost-effective enhancement of cocoa productivity. The adoption of such innovative pollination technologies, alongside ecological approaches to conserve natural pollinators, offers a promising strategy for achieving sustainable and consistent cocoa production.

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