# Explosive pollen release and pollination as a function of nectar-feeding activity of certain bees in the biodiesel plant, *Pongamia pinnata* (L.) Pierre (Fabaceae)

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**Pongamia pinnata is a dry-season bloomer. It produces nectariferous flowers with copious amount of pollen and additionally secretes nectar droplets on wing and keel petals. It has a peculiar explosive floral mechanism adapted for tripping by certain nectar-seeking bees. Such bees access nectar only if they cause keel explosion that results in pollination. The plant is primarily dependent on bee species such as *Apis dorsata*, *A. cerana indica*, *Amegilla* sp., *Megachile* sp., *Xylocopa latipes* and *X. pubescens* for pollination. Wasps also cause keel explosion and pollination, but they are occasional visitors only. Other bees and thrips also collect pollen and nectar droplets present on wing and keel petals; the former group acts primarily as pollen thieves and the latter also as nectar thieves. The flowers stay open only on the day of anthesis and remain closed for the other two successive days of flower-life. Unpollinated flowers fall off while pollinated ones develop into fruits.**

**Keywords:** Bee pollinators, explosive floral mechanism, nectar-feeding activity, *Pongamia pinnata*.

FLOWERING plants have developed various types of floral mechanisms to achieve pollination. The pollen transfer process has widely different aspects depending on whether the vector is an animal or an inanimate physical force. Each part of the flower functions in its own way, but the functions are correlated. Certain combinations of floral traits producing definite flower types appear more frequently, and one such type is the papilionaceous flower. This flower type shows adaptations with specific and highly efficient pollination mechanisms that have relationships with biotic pollen vectors. In Fabaceae, different pollination mechanisms adapted to different biotic vectors such as bees and birds have been reported[1–5]. Explosive pollination is one such mechanism, which occurs in *Cytisus scoparius*, *Medicago sativa*, *Ulex europaeus*, *Spartium*, *Canavalia* and *Mucuna* species[1]. This is a complicated pollination mechanism, which essentially requires tripping by specific biotic vectors to cause explosive release of pollen to result in pollination. In the absence of

flower-tripping agents, the flowers remain unpollinated and result in a breakdown of the pollination system[1].

In the present study, the functional morphology and floral syndrome of the flowers of *Pongamia pinnata* have been studied in view of its high commercial importance as a biodiesel plant in addition to several other uses[6–8]. It has been found to have a complicated floral mechanism for the violent release of pollen and stigma pollination synchronously, when tripped by specific bees. This floral mechanism adapted to pollination by certain nectar-feeding bees has been explained in the light of the relevant floral mechanisms.

Twenty-five trees of *P. pinnata* located at Lotugedda–Lambasingi Eastern Ghats forest site (lat. 17°52′N and long. 82°21′E), at an elevation of 900 m in Visakhapatnam district, Andhra Pradesh were studied during 2003–04. Leaf flushing and flowering season events were recorded by making periodical field trips to the study site. The flowering process and duration were noted at the level of individual trees by following twenty-five selected trees from the commencement to cessation of flowering. Ten inflorescences selected at random from different trees were tagged before the initiation of flowering and followed daily until they ceased flowering, to note the number of open flowers. The open flowers were then removed to avoid recounting on the next day. Twenty-five flowers were used to note floral characteristics. Pollen grain number/anther per flower was determined from twenty flowers distributed over five different individuals following the procedure in Solomon Raju and Subba Reddi[9]. Stigma receptivity was tested with $H_2O_2$ according to Dafni[10]. This procedure indicates that stigma produces bubbles if receptive. The speed of the bubbles varied during the receptive period. Emission of bubbles from the stigma surface with great speed was taken as strong receptivity, while the slow emission of bubbles as weak receptivity. The time of anthesis and anther dehiscence was noted by observing marked mature buds in the field. The ambient temperature and relative humidity were measured at the plant during the study period. The time and manner of anther dehiscence were noted using a 10× hand lens. Ten flowers from five trees were marked and bagged at mature bud stage, opened after anthesis and nectar squeezed into a micropipette in order to measure the volume of nectar at that time. The same procedure was followed using the same flowers at hourly intervals to measure nectar volume until the cessation of nectar production. Based on these data, the average volume of nectar per flower was determined and expressed in microlitre. The nectar sugar concentration was noted using a Hand Sugar Refractometer (Erma, Japan). Sugar composition was determined by paper chromatography using a butanol–acetone–water solvent and aniline hydrogen phthalate as developer. Standard solutions of glucose, fructose and sucrose were run simultaneously for comparison[11]. Flower behaviour during the entire period of its life was carefully observed

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**Figure 1.** Flowering phenology of *Pongamia pinnata* trees.

with reference to its pollination. Flower visitors were observed with respect to their mode of approach, landing, probing behaviour, forage collected, contact with sex organs to effect pollination and inter-tree foraging activity. Foraging visits made by bees at each hour were recorded on some selected flowering inflorescences. The same data were used for computing total daily visits made by each bee species. The length of a foraging visit per flower and the number of flowers foraged per minute were recorded for bee visitors to evaluate their foraging efficiency. Pollen pick-up by each bee species that visited the flowers was assessed through body washings in aniline blue. Based on these data, the role of different flower visitors in pollination was assessed.

In *P. pinnata*, leaf flushing occurs in March and flowering during April–May. A few individuals extend flowering into June. An individual tree blooms *en masse* continuously for about one month period (Figure 1). The inflorescence is a long raceme with $61 \pm 8$ flowers, which anthese acropetally over a period of $11 \pm 4$ days (Figure 2 *a*). The flowers appear quite conspicuous against the new foliage. A few trees show flowering during the second season in October–November. Such trees produce a few inflorescences at a time and flower for about two weeks. Rarely, one or two trees with a large number of inflorescences show profuse flowering for about one month.

The flowers are large, mildly fragrant, bisexual and zygomorphic. The calyx is dark purplish-brown and cup-like. The corolla is papilionaceous with two light-purple wing and two white keel petals and one greenish-white standard petal. The standard petal is broad with a light greenish-yellow nectar guide at the centre and hook-like

structures at the base; it is posterior in position and encloses the margins of wing petals, which in turn overlap on the margins of keel petals. The keel petals represent a boat-shaped structure in which the stamens and stigma are embedded (Figure 2 *i*). The stamens are ten, diadelphous with nine stamens united into one bundle and the tenth one in free condition. The bundled stamens form staminal tube at the base and the filaments become free towards the apex and bear monomorphic, dithecous anthers. All the ten stamens have a common origin at the flower base. The bundled stamens bend inward and form a conical-shaped tube at the extreme flower base, while the tenth stamen arises separately without any bending and forms open gaps on both sides towards the staminal tube. The tenth stamen is quite opposite to the standard petal. All the ten stamens have prominent upward arching. The ovary is semi-inferior with a single carpel having two (rarely one or three) ovules. It has a white style terminated with a small wet stigma; the terminal portion arches upwards and extends 2 mm beyond the height of the anthers (Figure 2 *j*).

Mature buds open during 0700–1000 h with peak anthesis at 0800 h. Unfolding of the standard petal indicates flower opening (Figure 2 *b*). The wing and keel petals do not unfold and remain in their original position as in mature bud stage. All the ten anthers dehisce by longitudinal slits in mature bud stage, approximately 3 h prior to anthesis. The number of pollen grains per anther is $2785 \pm 266$ and per flower 27,850. Nectar secretion begins inside the staminal tube at the base an hour after anthesis. Its secretion is continuous for 6 h during flower-life. The total nectar secretion period in the flowers that open on a given
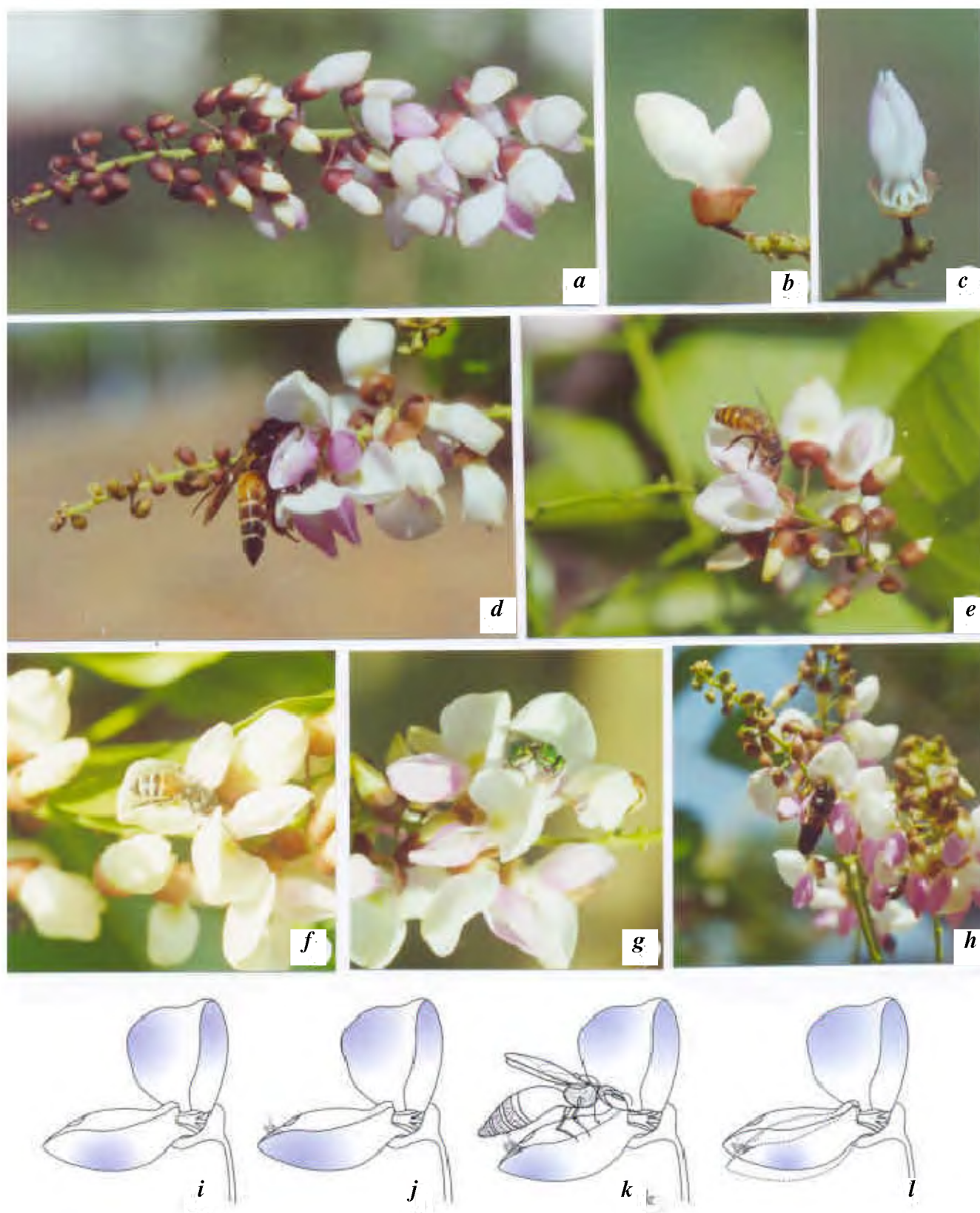
**Figure 2.** *P. pinnata*: *a*, Acropetal anthesis of inflorescence; *b*, Open flower; *c*, Deep-seated and protected nectar at flower base; *d–h*, Flower visitors – *d*, *Apis dorsata*; *e*, *A. cerana*; *f*, *A. florea*; *g*, *Pithitis binghami*; *h*, *Megachile* sp., *i–l*, Floral explosion caused by bees – *i*, Open flower with concealed sex organs in keel petals; *j*, Relative positions of stigma and stamens; *k*, Explosive release and contact of sex organs with bee's underside; *l*, Keel and wing petals taking their original position following departure of the bee.

**Table 1.** Nectar secretion pattern and sugar concentration in *Pongamia pinnata*

| Time | Nectar volume (μl) | | | | Sugar concentration (%) | | | | Temperature (°C) | Relative humidity (%) |
|------|-----|------|-----|-----|-----|------|-----|-----|------|------|
| | N | R | x̄ | SD | N | R | x̄ | SD | | |
| 0600 | 10 | Nectar secretion not initiated | | | 10 | Nectar secretion not initiated | | | 29.0 | 85 |
| 0700 | 10 | | 10 | | | | | | 30.5 | 80 |
| 0800 | 10 | 0.88–1.38 | 1.19 | 0.184 | 10 | 21–32 | 28.0 | 3.92 | 31.5 | 70 |
| 0900 | 10 | 0.87–1.00 | 0.93 | 0.048 | 10 | 26–41 | 32.0 | 4.73 | 32.4 | 69 |
| 1000 | 10 | 0.62–0.85 | 0.75 | 0.164 | 10 | 28–46 | 37.9 | 5.26 | 32.6 | 66 |
| 1100 | 10 | 0.20–0.74 | 0.42 | 0.194 | 10 | 31–51 | 39.3 | 5.58 | 33.0 | 64 |
| 1200 | 10 | 0.13–0.67 | 0.27 | 0.238 | 10 | 34–54 | 41.9 | 5.20 | 33.2 | 63 |
| 1300 | 10 | 0.00–0.63 | 0.15 | 0.238 | 10 | 35–51 | 43.5 | 4.45 | 34.6 | 61 |
| 1400 | No further nectar secretion | | | | 10 | 35–52 | 44.6 | 5.78 | 35.3 | 60 |
| 1500 | | | | | 10 | 35–59 | 95.2 | 6.96 | 34.2 | 62 |
| 1600 | | | | | 10 | 34–54 | 45.4 | 6.32 | 33.0 | 66 |
| 1700 | | | | | 10 | 35–55 | 45.5 | 6.21 | 32.0 | 68 |

N, No. of flowers observed; R, Range.

**Table 2.** Nectar droplets volume and sugar concentration on wing and keel petals of *Pongamia pinnata* flowers

| Time | Nectar volume (μl)/wing and keel petals in a flower | Sugar concentration (%) | Temperature (°C) | Relative humidity (%) |
|------|------|------|------|------|
| 0700 | – | – | 30.5 | 80 |
| 0800 | 0.03 | 13.4 | 31.5 | 70 |
| 0900 | 0.15 | 14.0 | 32.4 | 69 |
| 1200 | – | 14.4 | 33.2 | 63 |
| 1400 | – | 15.0 | 35.3 | 61 |
| 1600 | – | 15.2 | 32.5 | 64 |
| 1700 | – | 15.0 | 32.0 | 62 |

day falls between 0800 and 1300 h. The total amount of nectar produced per flower is 3.71 μl (Table 1). The nectar sugars included sucrose, glucose and fructose with the first as dominant and sugar concentration varies from 21 to 59% through the day, with the ambient temperature ranging from 29 to 35°C and relative humidity from 85 to 60% (Table 1). Nectar is concealed by the hook-like structures of the standard petal, which hold the basal part of wing and keel petals intact (Figure 2 c). In trees that show flowering in the second season, flowers produce 1.25 μl of nectar with 45–47% sugar concentration. Nectar production occurs during 0800–1200 h. The flowers also produce nectar droplets with 13–15% sugar concentration on the outer surface of the wing and keel petals during 0800–1200 h. These droplets amount to 0.18 μl per flower (Table 2). The stigma attains receptivity one hour after anther dehiscence, but strong receptivity occurs during 0900–1600 h. The flowers begin to close slowly from 1700 h onwards and close completely at 1800 h. Gradual movement of the standard petal to enclose the wing and keel petals completely indicates closure of the flower. The closed flowers remain so permanently and look similar to mature buds. In pollinated flowers, the corolla drops-off on the third day, staminal tube after 10 days and calyx after 20 days. The ovary gradually enlarges and grows into a fruit. Unpollinated flowers fall off on the third day.
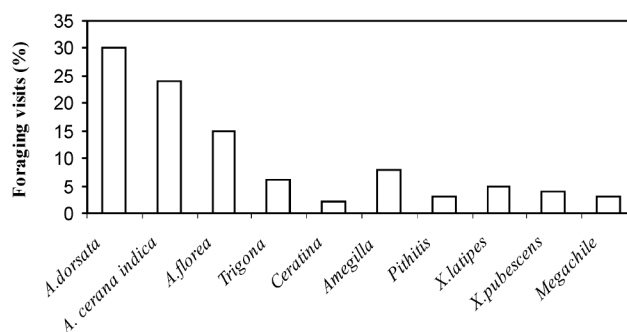


**Figure 3.** Per cent foraging visits of different bees on *P. pinnata*.

Flower visitors included bees [*Apis dorsata* (Figure 2 d), *A. cerana* (Figure 2 e), *A. florea* (Figure 2 f), *Trigona iridipennis*, *Ceratina simillima*, *Pithitis binghami* (Figure 2 g), *Amegilla* sp., *Xylocopa latipes*, *X. pubescens* and *Megachile* sp. (Figure 2 h)], wasps (*Sphex* sp., *Vespa* sp., *Ropalidia spatulata*, *Delta pyriformes*) and thrips (*Thrips hawaiiensis* and *Haplothrips tardus*). *Xylocopa* bees and wasps collected only nectar, while all other bees and thrips collected pollen, nectar and nectar droplets. Among bees, *Apis* and *Amegilla* made most of the visits (Figure 3). All visitors foraged throughout the day with more foraging activity during the forenoon hours, especially dur-
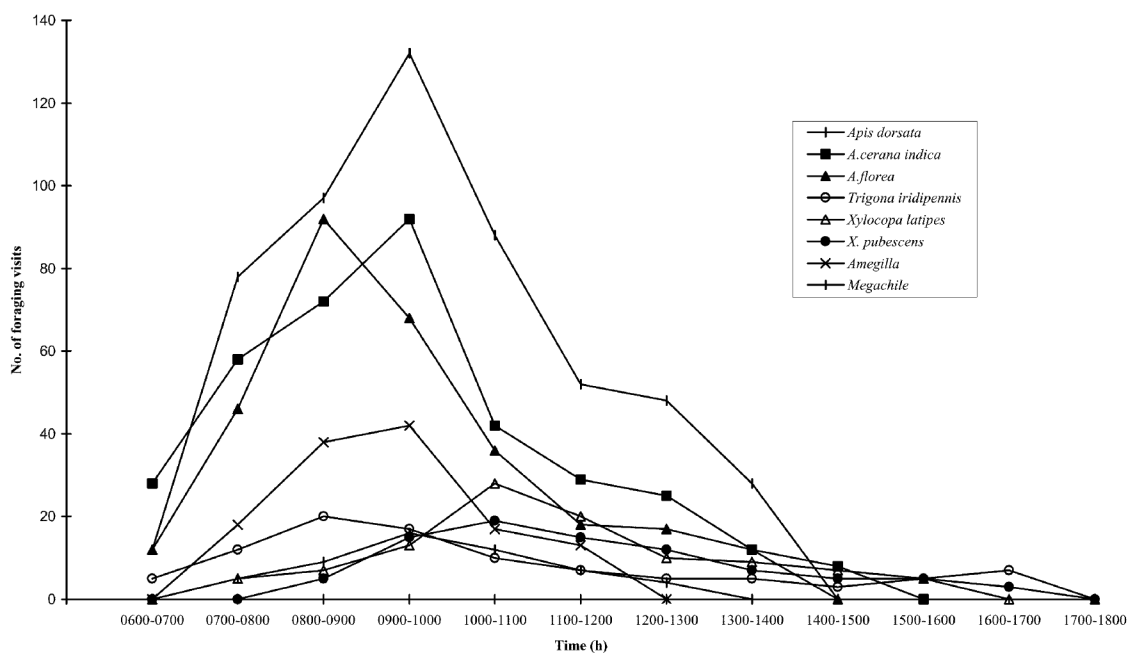
**Figure 4.** Hourly foraging activity of bees on *P. pinnata*.

ing nectar secretion period (Figure 4). All visitors probed the flowers from the front side without any side-working. Bees such as *Apis*, *Megachile*, *Amegilla* and *Xylocopa* on landing, landed depressed wing and keel petals and reached the nectar area for nectar collection, the stamens and stigma were released violently from the keel petals. Simultaneously, the stigma and pollen ejected explosively from the anthers stuck to the ventral side of these bees (Figure 2 *k*). *A. florea* was relatively inefficient in depressing keel petals to access nectar but it appeared to be successful mostly with previously visited flowers. To collect pollen, the same bees in the same or consecutive visits, gradually turned their head away from the standard petal and moved towards the location of the anthers and stigma. In doing so, they invariably contacted the stigma, effecting pollination. With the departure of these bees, the keel and wing petals returned to their original state concealing the nectar, stamens and stigma (Figure 2 *l*). Wasps also caused similar effect in flowers but their visits were occasional. Bees and wasps were found collecting floral rewards from different individuals, contributing to both self- and cross-pollination. The bees mentioned above were found to move between flowers fast, spending a small amount of time in search of more floral rewards (Table 3). Further, they also carried more pollen on their ventral side and honey bees, in addition, collected pollen in their pollen baskets situated on the third pair of legs (Table 4). The small bees, *Trigona*, *Ceratina* and *Pithitis* collected nectar droplets and pollen in the same manner as bees and wasps did during pollen collection but their pollen-collecting activity was ineffective to trip keel petals. They also proceeded gradually towards the standard petal in search of nectar. They were unable to depress keel petals

to access nectar. Thrips were resident foragers, moved freely within the flowers and collected nectar and pollen without tripping keel petals. Therefore, *Apis*, *Megachile*, *Amegilla* and *Xylocopa* bees were the principal pollinators.

Explosive pollination mechanism occurs in widely different plant families such as Lamiaceae[12], Fabaceae[13], Loranthaceae[14], Onagraceae[15], Rhizophoraceae[16,17], Marantaceae[18], Urticaceae[19], Ericaceae[20], Fumariaceae, Musaceae, Acanthaceae[21], Cornaceae[22] and Orchidaceae[21,23]. In some plants, the mature buds remain unopen with high tension and when tripped by bees or birds, they open and release the stamens and stigma explosively and synchronously and consequently, pollination occurs. In other plants such as the Fabaceae members, flower opening represents unfolding of the standard petal and the remaining unit remains under high tension with concealed stamens and stigma. When flower visitors arrive, the stamens and stigma release explosively at the same time, resulting in pollination. Among Fabaceous plants, *Medicago sativa*, *Cytisus scoparius*, *Ulex europaeus*, *Spartium* sp. and *Canavalia* sp. show explosive mechanisms with adaptations for tripping by certain bees[1]. In the present study, *P. pinnata* also exhibited explosive floral mechanism with certain special characteristics. In open flowers, the standard petal unfolds and faces the opposing wing and keel petals. The stamens and stigma are still concealed in the keel petals. Further, the nectar is also concealed due to hook-like structures present on the standard petal at its base, which hold the keel and wing petals firmly. Flower visitors require strength to depress the keel petals in order to have access to nectar; only those flower visitors which have the required strength to do so can get access to nectar and in the process, cause keel explosion and pollination. The

**Table 3.** Foraging efficiency of bees on *P. pinnata*

| Bees | No. of flower visits/min | | | | Length of a foraging visit (s) | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | N | R | $\bar{x}$ | SD | N | R | $\bar{x}$ | SD |
| *Apis dorsata* | 10 | 10–16 | 12.5 | 2.37 | 10 | 2–6 | 3.7 | 1.10 |
| *A. cerana indica* | 10 | 6–12 | 8.0 | 1.94 | 10 | 4–9 | 6.7 | 1.70 |
| *A. florea* | 10 | 5–9 | 6.4 | 1.21 | 10 | 4–11 | 8.1 | 1.41 |
| *Trigona iridipennis* | 10 | 3–7 | 4.7 | 1.00 | 10 | 6–15 | 10.6 | 2.72 |
| *Ceratina simillima* | 10 | 4–8 | 6.3 | 1.48 | 10 | 5–13 | 9.8 | 2.40 |
| *Pithitis binghami* | 10 | 3–7 | 5.8 | 1.66 | 10 | 7–12 | 8.6 | 1.90 |
| *Xylocopa latipes* | 10 | 8–13 | 10.3 | 1.73 | 10 | 2–4 | 2.9 | 0.84 |
| *X. pubescens* | 10 | 7–14 | 10.6 | 2.38 | 10 | 2–5 | 3.8 | 1.18 |
| *Amegilla* sp. | 10 | 10–18 | 14.0 | 2.36 | 10 | 2–4 | 2.8 | 0.74 |
| *Megachile* sp. | 10 | 6–11 | 8.2 | 1.65 | 10 | 5–9 | 6.2 | 1.37 |

N = No. of flowers observed; R = Range; $\bar{x}$ = Mean; S.D. = Standard deviation.

**Table 4.** Pollen pick-up efficiency of bees on *P. pinnata*

| Bees | Pollen grains found in bee body washings | | | |
| --- | --- | --- | --- | --- |
| | *N* | *R* | $\bar{x}$ | SD |
| *Apis dorsata* | 10 | 1240–4170 | 2464 | 813.9 |
| *A. cerana indica* | 10 | 430–2360 | 1193 | 534.4 |
| *A. florea* | 10 | 260–1760 | 874 | 542.2 |
| *T. iridipennis* | 10 | 68–420 | 213 | 128.2 |
| *Ceratina simillima* | 10 | 86–650 | 306 | 188.4 |
| *P. binghami* | 10 | 120–790 | 420 | 229.9 |
| *X. latipes* | 10 | 1260–6820 | 3325 | 1658.1 |
| *X. pubescens* | 10 | 1820–8600 | 4920 | 2113.4 |
| *Amegilla* sp. | 10 | 960–5200 | 3005 | 1509.3 |
| *Megachile* sp. | 10 | 1270–4220 | 2782 | 911.7 |

*N*, No. of insects observed; *R*, Range; $\bar{x}$, Mean pollen; S.D., Standard deviation.

study reveals that bees such as *A. dorsata*, *A. cerana indica*, *Amegilla* sp., *Megachile* sp., *X. latipes* and *X. pubescens* have the necessary strength to depress keel petals and access the nectar; they are only able to cause keel explosion. When these bees probe the flower in this manner, the stigma and stamens release explosively and synchronously from the tensed keel and forcibly strike the underside of the bees. Thus the bees get the full load of pollen under their body. As the stigma stands above the level of the stamens, it strikes the underside of the bees first and then the stamens. In effect, the stigma is most likely to receive cross-pollen first from the bodies of the bees and it may also receive some self-pollen during keel explosion. The pollination event ends with keel explosion and departure of the bees. The keel petals return to their original state concealing the stamens and stigma and the nectar following the departure of the bees. This state of the flower facilitates multiple visits by keel-tripping bees to ensure pollination success. These bees, except *X. latipes* and *X. pubescens* also effect pollination while collecting pollen. They are quite efficient to collect floral rewards by spending a short span of time per flower and make frequent visits between different individual trees in quest of more nectar and/or pollen. Such a foraging behaviour promotes cross-pollination. Further, these bees carry a good amount

of pollen on their bodies compared to other insects. Other bees such as *T. iridipennis*, *C. simillima* and *P. binghami* are small and do not cause keel explosion. They collect pollen and nectar droplets present on the wing and keel petals; in doing so they establish contact with the stigma and effect pollination. Although their pollen-feeding activity contributes to pollination, they deplete the amount of pollen to a great degree and hence act primarily as pollen thieves. Wasps cause keel explosion in their search for nectar and contribute to pollination, but they are occasional visitors only. Thrips being very small, move inside the flowers and have easy access to both nectar and pollen. They occur in great numbers at inflorescence level, deplete both floral rewards making them unavailable to some extent for the legitimate pollinators. However, their pollen-feeding activity may contribute to occasional self-pollination.

In *P. pinnata*, only long-tongued bees such as *A. dorsata*, *A. cerana indica*, *Megachile* sp., *Amegilla* sp., *X. latipes* and *X. pubescens* are found to have access to nectar, and in the process causing keel explosion and pollination. Having access to nectar, these bees must find nectar as energetically rewarding; otherwise they do not make successive visits to *P. pinnata* flowers. Bee flowers tend to produce high nectar sugar concentrations and honey bees,

in particular, prefer sugar concentrations of 30 to 50% (ref. 24). Bee flowers, especially long-tongued bee flowers, produce small volumes of nectar with large amounts of sugar with sucrose as the main constituent[24,25]. Further, it has been experimentally proved that honey bees prefer sucrose-rich nectars[24]. In *P. pinnata* also, the flowers produce a small volume of sucrose-rich nectar with high sugar concentration. This nectar satisfies the energetic requirement of probing bees that cause keel explosion. This finding agrees with previous works[24,25]. Environmental conditions have been reported to affect sugar concentrations in nectar by evaporation, and sugar concentrations increase through the day. The flowers at different heights on the same tree differ in nectar sugar concentration and sugar concentration is greater in upper flowers[24]. In *P. pinnata* too, similar situation exists and the sugar concentration changes greatly through the day. It can be expected that the upper flowers contain higher sugar concentrations in view of summer temperatures. The differences in nectar sugar concentrations at different times of the day and at different heights of the trees may have some significance in relation to the foraging activities of bees[26]. Foraging activity of bees in the present study is largely confined to the forenoon period and this can be related to the period of nectar secretion. The nectar droplets on wing and keel petals with less sugar concentration appear to have some importance in protecting the sex organs against withering. At the same time, these droplets act as a secondary floral reward to bees which fail to collect deeply seated and protected nectar. All bees collect pollen, which is plentiful at the flower level. Lakshmi *et al.*[27] reported that *P. pinnata* pollen and nectar are good honey bee forage during summer season. They also described pollen grain characteristics, suggesting that the grains are small, tricolporate and adhere in clumps. It is easy for the bees to collect and keep them in their pollen baskets. Gottsberger[28] reported that pollen morphology plays an important role in relation to pollinators but it is a field still to be explored. Nevertheless, *P. pinnata* is an important bee-forage tree species during summer season.

The study shows that *P. pinnata* has developed a complicated explosive keel mechanism intended for tripping by certain nectar-seeking bees. These bees initially concentrate on how to handle such flowers to access nectar and later on habituate themselves to probe the flowers successfully for collecting nectar. This suggests that the floral mechanism in *P. pinnata* is specialized and only those bees which are able to work out floral configuration and cause keel explosion, can get access to nectar. Further, such an explosive floral mechanism is no doubt an important floral adaptation to discourage self-pollination and promote cross-pollination. The flower stays open only on the day of anthesis. At the end of the day, it closes whether pollinated or unpollinated and remains so until flower drop in unpollinated flowers. Such flowers look like mature buds. Further, the stigma stays receptive from mature bud onwards and loses its receptivity shortly before the closure of the flower. This indicates that pollination should occur only during flower-opening period and pollinator bees should visit during this period only. These phenomena suggest that *P. pinnata* is a specialist with highly intricate pollination mechanism adapted to certain nectar-seeking bees. But, such a pollination mechanism is non-functional in the absence or rarity of pollinator bees, and it will surely reflect in fruit set rate. Retention of unpollinated flowers for two consecutive days appears to have a specific role for the plant. They may allow the remobilization and recycling of structural proteins and nutrients from flowers back to the plant and serve as an energy-efficient means of enhancing the overall attractiveness of the inflorescence or plant to pollinators[29]. Unpollinated dead flowers are more in number and litter the ground, representing a breakdown of the specialized pollination system. Other factors such as pollen limitation and lack of pollen germination during pre-fertilization stage[30,31], selective elimination of self-pollinated fruits and competition for limited maternal energy resources among fertilized ovules leading to abortion during post-fertilization stage[32], and also external energy resource environment in which the plant is growing[33] regulate fruit set rate and hence success of sexual reproduction in *P. pinnata*.

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# Nutrient budgets for Muthupet lagoon, southeastern India

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**Budgets of nitrogen and phosphorus from the semi-enclosed Muthupet lagoon were constructed through monsoon observations and modelling. The lagoon is a shallow water body and hence surface water samples associated with the lagoon were collected and measured for hydrochemical properties, inorganic and organic nutrients (dissolved inorganic nitrogen, dissolved organic nitrogen, dissolved inorganic phosphorus and dissolved organic phorphorus). The average inorganic N and P concentrations of the lagoon were almost equal to that of their river concentrations, while organic phosphorus was lower by 30% and organic nitrogen was higher by 26%. Terrestrial inputs through run-off, mixing and residual fluxes were dominant forcing mechanisms in maintaining lagoon nutrient concentrations. Water exchange time of the lagoon was estimated at 1.4 days. However, the nutrient, especially DIP, DIN and DON, exchange time was higher by approximately 50% of water exchange time, whereas the same for DOP was half that of water exchange time. The nonconservative fluxes $\Delta$DIP, $\Delta$DOP, $\Delta$DIN and $\Delta$DON from the lagoon were 0.03, –0.06, 0.92 and 5.28 mmol $m^{-2} d^{-1}$ respectively, inferring that DIP, DIN and DON were removed from the system when DOP was added to it.**

**Keywords:** Exchange time, nutrient budgets, non-conservative fluxes.

ANTHROPOGENIC nutrient inputs, in recent decades, into coastal seas have generally increased steadily[1–3], a phenomenon that may enhance primary production and provide an additional sink for atmospheric carbon. Simultaneously, however, natural and human-derived organic matter discharged into coastal seas may be partially or totally respired, providing a source of carbon dioxide. Despite difficulty in obtaining carbon and nutrient budgets through direct observations and syntheses, biogeochemists have employed various models to simulate nutrient and carbon budgets in well-defined systems, applying simplified calculations to existing data[4–8]. Meanwhile, LOICZ (Land–Ocean Interactions in the Coastal Zone) has developed