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POLLINATION ECOLOGY OF OVIPAROUS SEMI-EVERGREEN MANGROVE TREE SPECIES, *XYLOCARPUS GRANATUM* KOEN AND *X. MEKONGENSIS PIERRE.* (MELIACEAE) AT CORINGA MANGROVE FOREST, ANDHRA PRADESH, INDIA

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Abstract - *Xylocarpus granatum* and *X. mekongensis* are semi-evergreen tree species. Both species exhibit leaf fall, leaf flushing, flowering and fruiting sequentially. They are seasonal bloomers but also flower sporadically almost throughout the year. The flowers are functionally monoecious and exclusively pollinator-dependent. In cymes, the terminal flower is usually pistillate while the lateral ones are usually staminate. In *X. mekongensis*, solitary flowers are usually pistillate. In both, the pistillate and staminate flowers produce stamens with dehiscent anthers but ovary is functional only in the former while pollen is fertile only in the latter. Hawk moths are principal pollinators while butterflies and bees are supplementary pollinators in both plant species. Both species fruit through geitonogamy and xenogamy and fruit set in open-pollination is very low which could be attributable to unknown inherent regulatory mechanisms, delicate inflorescence and the production of a few pistillate flowers at plant level. The study suggests that there is an urgent need to protect the surviving trees and take measures to restore the populations of both the species.

Keywords: *Xylocarpus granatum*; *Xylocarpus mekongensis*; monoecy; hawk moths; butterflies; bees; geitonogamy; xenogamy

Introduction

Xylocarpus is the only mangrove genus in Meliaceae family (Filippos, 2018). This genus has distinct moderate-sized evergreen or deciduous monoecious or dioecious tree species with well developed woody trunk yielding valuable timber: *X. granatum, X. mekongensis* and *X. moluccensis* which are distributed in the tropical tidal forests of the Old World, typically in the mangrove habitat or in sandy or coastal habitat spreading from Africa to Australia through India and Malayan Archipelago (Tomlinson, 1986). Several authors (Singh & Garge, 1993, Banerjee et al., 1989, Banerjee & Rao, 1990, Deshmukh, 1991) stated that all the three species of *Xylocarpus* occur on the Andaman Islands and Orissa coast while *X. granatum* and *X. mekongensis* occur in the Sunder bans and Tamil Nadu coast. Kathiresan (2003) reported that *X. mekongensis* is restricted to West Bengal, Orissa and Andaman while *X. molluccensis* to Andaman only; these species have been reported to be threatened in India by Kathiresan (2008). Jugale et al. (2009) stated that *X. granatum* is a critically endangered species of Maharashtra and represented by a few individuals only. In Orissa, *X. granatum* and *X. mekongensis* bloom for a prolonged period and/or throughout the year; individual plants display different stages of flowering and fruiting (Banerjee & Rao, 1990, Upadhyay & Mishra, 2010). In Godavari mangrove wetland, *X. granatum* is rare in occurrence and represented by ten individuals only while *X. mekongensis* is very uncommon and represented by several individuals; the former is briefly deciduous and blooms during June-July while the latter is evergreen and blooms during August-September.

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These two species can be distinguished by their root, trunk, bark, leaves, inflorescence and fruit characters in the field. They are exploited for their timber in this area (Raju, 2003). In *X. granatum,* the bark is used for dysentery, diarrhoea and other abdominal troubles; the fruit as cure for swellings of the breast and elephantiasis (Yusuf et al., 1994) and the seed oil for hair illumination (Ghosh et al., 2008). *X. mekongensis* is tannin-rich and used for tanning heavy hides, toughening fishing nets and dying cloth; its wood is used for boat building, nails, house-posts, furniture and firewood (Pawar et al., 2013). Tomlinson (1986) reported that in mangroves, plant species with hermaphroditic sexual system are common while those with dioecious and monoecious sexual system are rare. *Xylocarpus* is monoecious which is represented by morphologically bisexual but functionally unisexual flowers with the nectar as the sole reward for the foragers. Further, he mentioned that this genus is bee-pollinated. Venkatesan (2011) reported that the mangrove honey samples in Sundarbans (Bangladesh) and Little Andaman (India) contained *X. granatum* pollen as secondary pollen type suggesting that honey bees use this species as pollen source. Almazol & Cervancia (2013) reported on the pollination of *X. granatum* in Philippines. These authors documented that *X. granatum* is an obligate out-crosser and its flowers display moth-adapted floral traits. Accordingly, moths act as principal pollinators while flies as supplementary pollinators. There is no information on the pollination biology of the other two species, *X. moluccensis* and *X. mekongensis* from any part of the world where these species are distributed. Keeping such a state of information on *Xylocarpus* in view, the present study has been contemplated to provide the details of pollination biology of *X. granatum* and *X. mekongensis* occurring in Coringa mangrove forest located in Andhra Pradesh State, India. The objectives of the study include the investigation of the floral biology to understand the floral syndrome and sexual system; functionality of floral syndrome with reference to pollinators visiting the flowers for floral reward(s); and to document the fruit set rate in both the species.

MATERIALS AND METHODS

Study area

The Coringa mangrove wetland lies between 16°30'-17°00'N and 82°10'-80°23'E in the State of Andhra Pradesh, India. In this wetland, *Xylocarpus granatum* and *X. mekongensis* is sparsely distributed from polyhaline to euhaline zone and represented by a few individuals only. These species are semi-evergreen with leaf fall, leaf flushing, flowering and fruiting taking place sequentially. Field as well as lab-work was made during April 2017 to December 2018.

Phenology and floral biology

The time and duration of each phenological event were recorded for both the plant species based on regular field trips made to their locations. Observations regarding the organization of inflorescences, the spatial positioning of flowers, and their position (terminal, axillary, etc.) on the plants were made since these features are important for foraging and effecting pollination by flower-visitors. The flower life was recorded by marking twenty mature buds on each plant species and following them until they dropped off. Anthesis schedule was recorded by observing twenty marked mature buds on each plant species in the field. The same mature buds were followed for recording the time and mode of anther dehiscence. The details of flower morphology such as flower sex, shape, size, colour, odour, calyx, corolla, stamens and ovary were described based on twenty flowers collected randomly from five individual plants for each species. The stigma receptivity was observed by H_2O_2 test. The period of slow release of bubbles from the surface of stigma following the application of hydrogen peroxide was taken as stigma receptivity.

Breeding systems and fruiting ecology

In *X. granatum* and *X. mekongensis,* the number of pistillate flowers used for geitonogamy, xenogamy and open-pollination to record fruit set rate was given in Table 1. Pistillate flowers were hand-pollinated with the pollen of staminate flowers of the same plant to test geitonogamy. Pistillate flowers were hand-pollinated with the pollen of staminate flowers of different plants to test xenogamy. These flowers were bagged and followed to record fruit set rate in these two modes. Further, pistillate flowers were tagged and followed to record fruit set rate in open-pollinations. Fruit maturation period, fruit dehiscence and seed dispersal were observed in the field to record fruit and seed characters in both plant species.

Table 1. Number of pistillate flowers used for geitonogamy, xenogamy and open-pollination to record fruit set rate in *X. granatum* and X. *mekongensi*.

Pollination mode	No. of flowers pistillate pollinated	No. of fruits formed	Fruit set (%)
X. granatum			
Geitonogamy	30	8	27
Xenogamy	30	11	37
Open-pollination	50	9	12
X. mekongensis			
Geitonogamy	30	7	23
Xenogamy	30	9	30
Open-pollination	50	8	16

Flower visitors and pollination

The insect species visiting the flowers of both plant species were observed and recorded during their flowering season. The hourly foraging visits of each insect species were recorded on three different days for each plant species and the data was tabulated to use the same for further analysis. The foraging visits were recorded for ten minutes at each hour during 05:00-18:00 h. The data obtained was used to calculate the percentage of foraging visits made by each insect species per day and also to calculate the percentage of foraging visits of each category of insects per day in order to understand the relative importance of each insect species or category of insects in pollination. The foraging behaviour of insect species was observed for 30 hours spread over three different days for the mode of approach, landing, probing behaviour, the type of forage collected, contact with essential organs to result in pollination, inter-plant foraging activity in terms of cross-pollination. The flower visitors captured during 10:00-12:00 h and during 16:00-18:00 h were brought to the laboratory. For each insect species, 10 specimens were captured and each specimen was washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present. In case of bees, pollen from pollen baskets was removed prior to washing them in ethyl alcohol. From this, the average number of pollen grains carried by each insect species was calculated to know the pollen carryover efficiency of different insect species.

RESULTS

Phenology

Xylocarpus granatum and *X. mekongensis* are semi-evergreen tree species and represented by a few individuals in Coringa Mangrove forest. Individuals of these species occur scattered here and there from polyhaline zone to euhaline zone along the edges of brackish water creeks. In *X. granatum*, the bark is light brown to light pink-orange, smooth and peels off as flakes when slits or cracks develop. In *X. mekongensis*, the bark is dark brown and peels off as long thick narrow strips. In both species, leaf fall, leaf flushing, flowering and fruiting events occur sequentially without any time gap. Initiation and completion of leaf shedding takes place in May (Fig. 1a). Leaf flushing occurs during the 1st week of June- and/or 2nd week of July (Fig. 1b). Floral buds also develop in synchrony with leaf flushing. First flowers appear in the last week of June; peak flowering occurs in July and gradually flowering ceases by the first or second week of August (Fig. 1c-e). Individual plants flower for 3-4 weeks. Further, sporadic flowering occurs on certain branches of individual plants outside this flowering period from September to March. In both the species, the duration between flower bud initiation and maturation is about 3-4 weeks only. Fertilized flowers initiate fruit development immediately and mature in about 3 months period. Usually, the plants fruit mostly during seasonal flowering.

Floral biology

In both species, the inflorescence is a forked flowering shoot with indistinct main axis which develops from the leaf axils. It produces several 3-flowered cymes on a zig-zag 6-8 cm long peduncle in *X. granatum* (Fig. 1f). In *X. mekongensis*, the inflorescence is a 10-12 cm long dense cymose panicle consisting of several 3-flowered cymes and an odd solitary flower between cymes. The pedicels are longer and the flowers are larger in *X. granatum* than those in *X. mekongensis*. The inflorescence characters are useful to distinguish the two species in the field. In both species, the 3-flowered cymes in both the species produce morphologically bisexual but functionally unisexual flowers which are either pistillate or staminate. Individual cymes do not produce all the three flowers on the same day; the terminal bud matures and opens first (Fig. 1g,h) while the lateral two buds mature and open on the next day or subsequent day. The entire inflorescence flowers for 7-10 days in both the species. The terminal flower is usually pistillate (Fig. 1i,j) while the lateral ones are staminate but there are also rare situations of terminal flower acting as staminate and one of the lateral flowers acting as pistillate. In *X. mekongensis*, the odd solitary flowers borne between cymes are usually pistillate and rarely staminate. The sexual system in both the species is monoecious.

Flower morphology

In both species, pistillate and staminate flowers are similar in shape and structure but they are different in the function of female and male organs. The pistillate flowers are 75 mm long in *X. granatum* and 50 mm long in *X. mekongensis*. The staminate flowers are 1-2 mm smaller than pistillate ones in both the species. In pistillate flowers, the ovary is robust with functional ovules (Fig. 1k) while the stamens are dehiscent but contain sterile pollen. In staminate flowers, the stamens are dehiscent and contain fertile pollen and ovary is slender with rudimentary ovules (Fig. 1l). The flowers of both sexes are pedicellate, fragrant, creamy white and actinomorphic. The calyx has four free sepals which are of equal length, cup-shaped at the tip, smooth at the base and shiny, especially during sunlight. The corolla has eight united

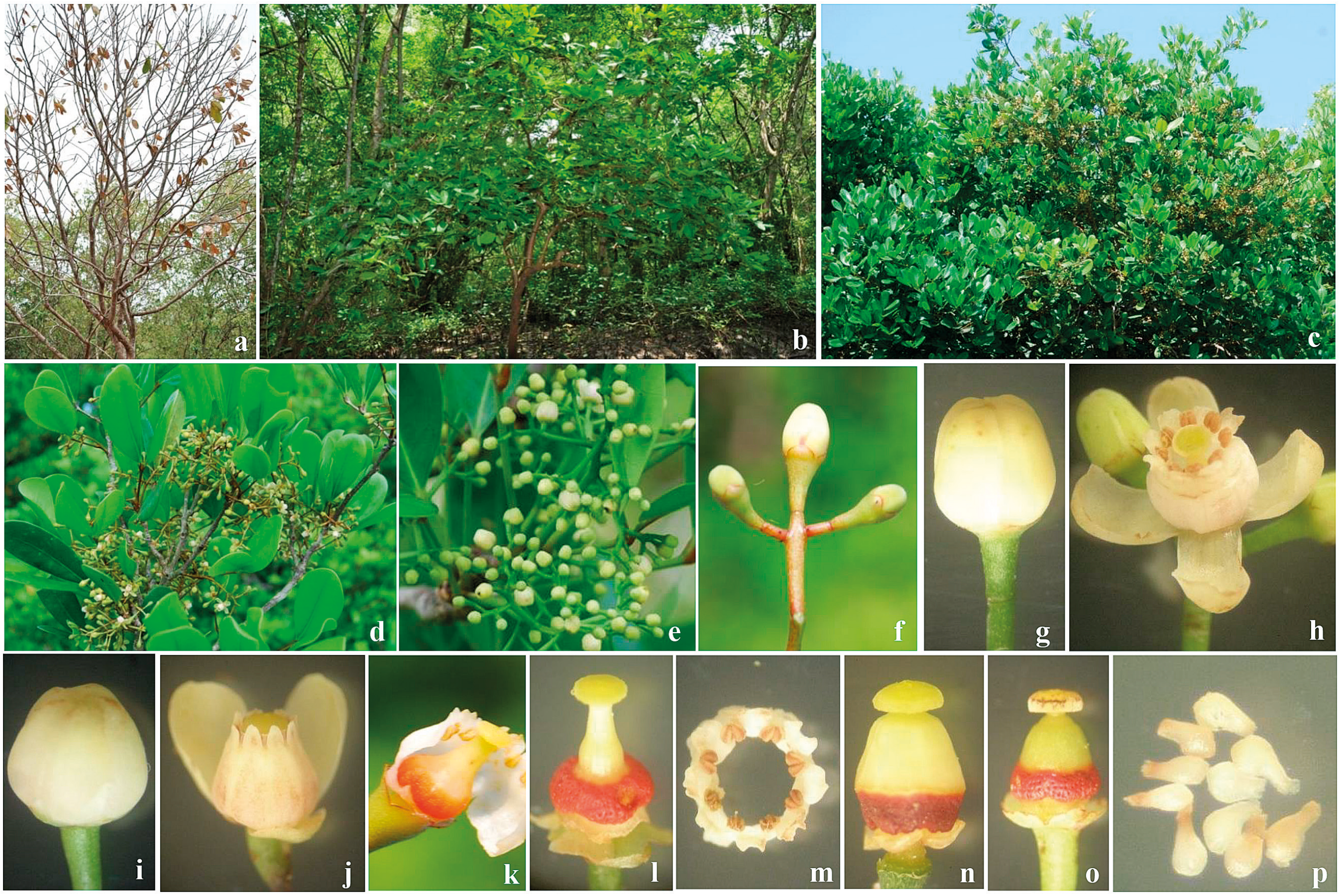

Figure 1. (a) *X. mekongensis* leaf shedding phase, (b) *X. mekongensis* leaf flushing phase, (c) *X. granatum* flowering tree, (d) *X. granatum* flowering branches, (e) *X. mekongensis* flowering phase, (f) *X. granatum* 3-flowered cyme with terminal flower maturing first, (g) *X. granatum* terminal mature bud, (h) *X. granatum* pistillate flower, (i) *X. mekongensis* pistillate mature bud, (j) *X. mekongensis* pistillate flower, (k) *X. granatum* pistillate flower with well-developed ovary, (l) *X. granatum* slender ovary, style and stigma surrounded by nectary disc in staminate flower, (m) *X. granatum* epipetalous stamens, (n) *X. mekongensis* well-developed gynoecium in pistillate flower, (o) *X. mekongensis* slender gynoecium in staminate flower, (p) *X. granatum* ovules in pistillate flowers.

Figure 2. (a) *X. mekongensis* ovules in pistillate flowers, (b) *X. granatum* pollen grain, (c) *X. mekongensis* pollen grain, (d) *Apis dorsata* collecting pollen from *X. mekongensis* flowers, (e) *Ceratina binghami* collecting pollen from *X. mekongensis* flowers, (f) *Euploea core* collecting nectar from *X. mekongensis* flowers, (g) *X. granatum* immature fruit, (h) *X. granatum* with fruit set, (i) *X. mekongensis* fruit dehiscence, (j) *X. mekongensis* seeds.

petals forming globose tube with basal periphery larger than apical periphery. The stamens are eight, epipetalous, sessile, and anthers dithecous which are attached at the notch of apical lobes of the corolla (Fig. 1m). The ovary is globose with short style and discoid stigma which blocks the mouth of the corolla (Fig. 1n); it is slender in staminate flowers of both the species (Fig. 1o). It has eight carpels and each carpel has a single chamber containing two ovules arranged on axile placentation (Fig. 1p, 2a). The stigma margin is crenulate and its upper surface has four radiating grooves. A fleshy cushion-shaped orange-red nectary disc present around the ovary base is quite prominent and united with the ovary.

Flower function

In both species, mature buds gradually open and take about 30-40 minutes from partial to completing opening. The anthesis occurs during 1600-1830 h. The pistillate and staminate flowers are produced simultaneously on the same and different inflorescences of the same plant. The nectar is secreted in minute volume around the ovary base and concealed completely by discoid stigma which nearly blocks the corolla mouth. In staminate and pistillate flowers of both species, the anthers dehisce by longitudinal slits nearly in synchrony with anthesis; the pollen in staminate flowers is fertile while that in pistillate flowers is sterile. In both species, the pollen grains in staminate flowers are creamy yellow, powdery, tetra zonocolporate with perforate ornamentation and psilate membrane; the grain size varies from 25.30 to 33.80 µm on polar axis and from 27.30 to 38.40 µm on equatorial axis (Fig. 2b,c). *In vitro* pollen germination test with 15% sucrose concentration indicated that pollen grains are viable 100% on the day of anthesis in both species but pollen showed 55% viability in *X. granatum* and 49% viability in *X. mekongensis* by the evening of the following day. In both species, pollen was non-viable on the 3rd day. In pistillate flowers of both the species, the stigma is receptive immediately after anthesis and loses receptivity by the evening of the following day. The pistillate and staminate flowers remain in their place for 2 days and fall off on the 3rd day.

Breeding system

Hand-pollination tests indicated that both *X. granatum* and *X. mekongensis* set fruit through geitonogamy and xenogamy. In *X. granatum*, the fruit set rate was 27% in geitonogamy and 37% in xenogamy. The corresponding fruit set percentages for *X. mekongensis* were 23% and 30% respectively. Fruit set in open-pollination was 18% in *X. granatum* and 16% in *X. mekongensis* (Table 1).

Flower visitors and pollination

In *X. granatum* and *X. mekongensis*, both pistillate and staminate flowers were foraged indiscriminately by flower visitors. The hawk moths such as *Agrius convolvuli* L., *Cephonodes hylas* L., *Macroglossum sitiene* Walker, *M. gyrans* Walker and *Nephele hespera* Fabr. (all belong to family Sphingidae of Order Lepidoptera) visited the flowers as soon as they opened in the late evening from 1600-1800 h and again during dawn and dusk hours (05:00-07:00 h and 16:00-18:00 h) of the following day for nectar collection. They hovered at the flowers and inserted their proboscis through the space between stigma margin and edge of the corolla mouth where the stamens were inserted to access the flower base to collect nectar. In so doing, the proboscis of hawk moths contacted the receptive stigmatic grooves in pistillate flowers and the dehisced anthers in staminate flowers invariably. In this foraging act, the hawk moths transferred pollen from staminate to pistillate flowers either on the same plant or on different conspecific plants and in effect pollination occurred. They swiftly moved from flower to flower on the same and different plants effecting both geitonogamy and xenogamy. During day time, the flowers of both the species were foraged by bees (*Apis dorsata* F. (Fig. 2d)*, A. cerana* F.*, A. florea* F. and *Ceratina binghami* Cockerell) (Fig. 2e) from 07:00 h to 17:00 h with maximum foraging activity during 07:00-10:00 h and during 16:00-17:00 h while butterflies (*Captopsilia pyranthe* L., *Eurema hecabe* L. and *Euploea core* Cramer) (Fig. 2f) from 07:00 h to 12:00 h with maximum foraging activity during 07:00-10:00 h (Fig. 3 and Fig. 4).

Of the total foraging visits made by insects, bees made 44%, hawk moths 33% and butterflies 23% (Fig. 5) in *X. granatum*. The corresponding percentages of foraging visits by these insects in that order were 42%, 36% and 22% in *X. mekongensis* (Fig. 5).

All bees belong to Apidae family of Order Hymenoptera. Among butterflies, *C. pyranthe* and *E. hecabe* belong to Pieridae family while *E. core* belongs to Nymphalidae family of the Order Lepidoptera. Bees approached the flowers in upright position, landed on the sepals and then moved to the corolla mouth to collect pollen from the anthers. They visited both pistillate and staminate flowers indiscriminately to collect pollen but only staminate flowers provided pollen for them. This pollen collection activity by bees resulted in the transfer of pollen from the bee body to the receptive stigma in pistillate flowers with pollination as end result. The bees tended to stay more time on the staminate flowers for pollen collection and less time on pistillate flowers, the differential behavior of which was recorded as non-availability of pollen from pistillate flowers. They never attempted to collect nectar due to mismatch between the

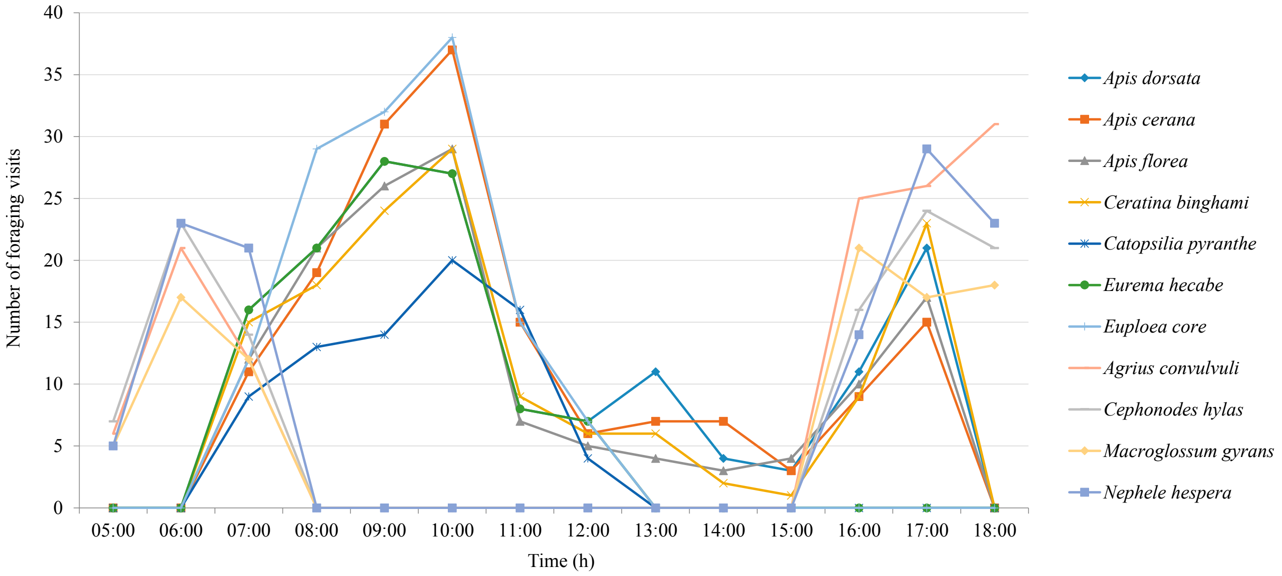

Figure 3. Hourly foraging activity of insect foragers on *Xylocarpus granatum.*

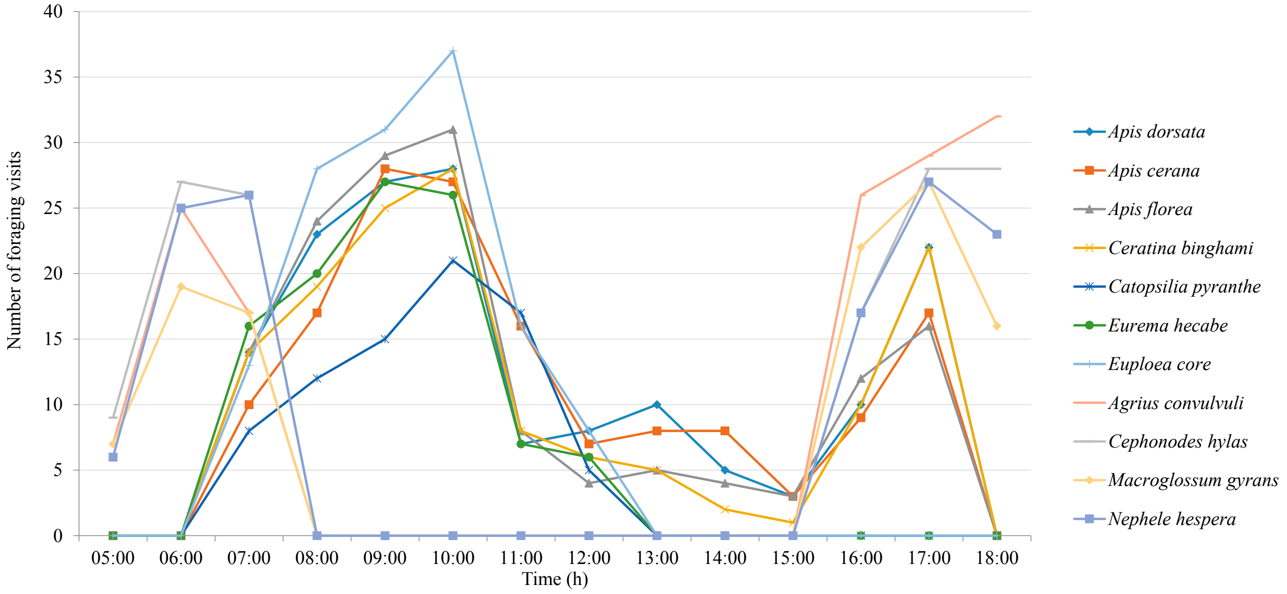

Figure 4. Hourly foraging activity of insect foragers on *Xylocarpus mekongensis.*

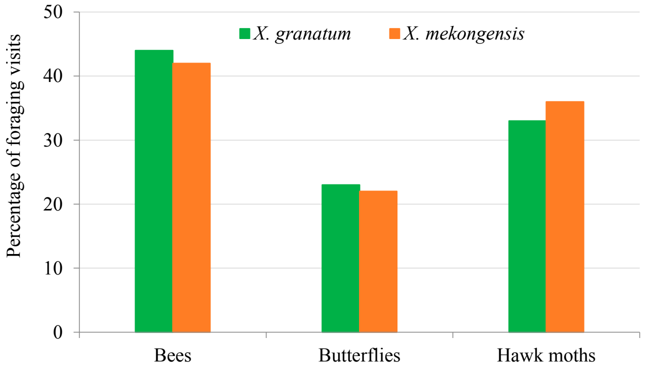

Figure 5. Percentage of foraging visits of insects on *X. granatum* and *X. mekongensis.*

tongue length and the corolla tube length, and also to the availability of narrow space between the margin of discoid stigma and the rim of the corolla mouth. Butterflies landed on the flowers/inflorescence and probed individual flowers for nectar; the flower probing behavior is exactly similar to that of the hawk moths which also collected nectar only. They foraged both pistillate and staminate flowers of both the species and effected pollination while collecting nectar. They moved from flower to flower slowly to collect nectar from the same and different conspecific plants and effected both geitonogamy and xenogamy in both the plant species. The body washings of all insects foraging on the flowers of both *X. granatum* and *X. mekongensis* showed that all

Table 2. Pollen recorded in the body washings of insect foragers on *Xylocarpus granatum* and *X. mekongensis*.

Insect species	Sample size (N)	*X. granatum*			*X. mekongensis*		
		Range	Mean	S.D.	Range	Mean	S.D.
Bees							
Apis dorsata	10	67-302	162.1	75.49	73 - 214	139.6	35.17
Apis cerana	10	54-209	115.5	50.08	56 - 182	121.1	29.35
Apis florea	10	93-157	99.2	19.44	29 - 60	46.8	8.29
Pithitis binghami	10	95-129	98.1	12.23	37 - 95	68.8	16.32
Butterflies							
Catopsilia pyranthe	10	22-47	31.8	7.38	24 - 62	46.4	10.23
Eurema hecabe	10	34-69	45.3	10.00	12 - 44	26.7	7.98
Euploea core	10	15-53	32.9	11.39	18 - 53	30.9	8.79
Hawk moths							
Agrius convolvuli	10	76-281	168.2	67.62	94-231	181.6	36.85
Cephonodes hylas	10	58-185	125.4	48.87	66-156	117.7	24.68
Macroglossum sitiene	10	45-78	40.2	9.05	52-103	76.6	12.88
Macroglossum gyrans	10	52-69	33.6	7.31	63-115	97.1	14.12
Nephele hespera	10	23-64	37.4	11.48	87-162	121.5	23.77

species carry pollen and transfer pollen from staminate to pistillate flowers. In *X. granatum*, the average pollen carried by bees ranged from 98.1 to 162.1, by butterflies from 31.8 to 45.3 and by hawk moths from 33.6 to 168.2. In *X. mekongensis*, the average pollen carried by bees ranged from 46.8 to 139.6, by butterflies from 30.9 to 46.5 and by hawk moths from 76.6 to 181.6 (Table 2). Therefore, hawk moths were treated as principal pollinators while bees and butterflies as supplementary pollinators.

In this mangrove ecosystem, this plant species was not visited during my field observations by any other insect species for pollen and/or nectar and for feeding on floral parts, especially delicate corolla.

Fruiting ecology

In both species, after fertilization, the ovary gradually bulges and produces seeds. Fruits mature in three months, they are green initially (Figure 2g) and reddish brown when mature. Individual paniculate cymes produce 1-3 fruits indicating that many terminal pistillate flowers of 3-flowered cymes do not end up in fruit set (Figure 2h). Fruits are pendulous, globose, large and woody; they are 8-10 cm across in *X. granatum* and 6-8 cm across in *X. mekongensis*. Fruits produce 8-12 seeds which measure 7.23 cm in length in *X. granatum* and 5-8 seeds which measure 5.8 cm in length in *X. mekongensis* but they are tetrahedral or angular and have corky seed coat and extruded radicle in both the species. Ripe fruits show cracks near ridges initially and eventually split into four parts from the apex to the base to release seeds (Figure 2i, j). As a result, the seeds fall off the trees, shatter and float away in tidal water. They begin to germinate while they are still in floating stage and before anchoring to the substratum.

DISCUSSION

The timing of sexual reproduction in mangrove plant species depends on local environmental conditions and differs broadly over the range of a species (Ali, 2016). The day length controls flowering while air temperature sets the period for fruit maturation in mangroves (Farrant et al., 1992; 1993). In the non-viviparous mangrove species, *Xylocarpus granatum* and *X. mekongensis*, the flowering seasons have been reported variously by different authors. In Philippines, Almazol & Cervancia (2013) reported that *X. granatum* displays two or three flowering seasons in a year. In India, Banjerjee & Rao (1990) reported that *X. granatum* flowers throughout the year in the mangrove forests of Orissa coast. Upadhyay & Mishra (2010) reported that *X. granatum* and *X. mekongensis* commence flowering in September and flowers continuously for a prolonged period in the mangrove forests of Orissa coast. Raju (2003) reported that *X. granatum* and *X. mekongensis* are seasonal bloomers; the former is an evergreen species and blooms during August-September while the latter is a deciduous species and blooms during June-July in Coringa Mangrove Forest, Andhra Pradesh, India. The present study conducted in the same forest showed that both *X. granatum* and *X. mekongensis* are semi-evergreen species and exhibit leaf fall, leaf flushing, flowering and fruiting aspects sequentially without any time gap. They are seasonal bloomers with flowering during June-August but sporadic flowering also occurs on certain branches of individual plants outside this flowering season except April-May. Further, the fruiting season is well defined and mature fruits disperse seeds in October. However, sporadic flowering contributes to the production of fruits by the plants almost throughout the year. Therefore, seasonal flowering and aseasonal sporadic flowering make the plants to display different stages of floral bud initiation, flowering, fruit initiation, maturing and mature fruits throughout the year.

Tomlinson (1986) reported that the genus *Xylocarpus* produces 3-flowered cymes with the terminal flower often female and opens first while the lateral flowers are male and open later. Further, he also stated that female flowers produce sterile pollen while male flowers produce non-functional ovules. Raju (2003) described the inflorescence and floral traits of *X. granatum* and *X. mekongensis* but he has not mentioned the sexuality of flowers in these species. Almazol & Cervancia (2013) reported on the floral biology and pollination in *X. granatum* without any mention of floral sexuality. The present study indicates that *X. granatum* and *X. mekongensis* produce axillary paniculate 3-flowered cymes with the terminal flower usually pistillate and opening first while the lateral ones usually staminate and opening later. Further, *X. mekongensis* produces solitary flowers between 3-flowered cymes and these flowers are usually pistillate. In both species, the pistillate and staminate flowers produce stamens with dehiscent anthers but pollen is fertile in staminate flowers only. Further, the two flower sexes produce ovary with ovules, style and stigma but only pistillate flowers have well developed ovary with functional ovules. The terminology of "male" and "female" for flower sexes in these species is irrelevant because all flowers have both male and female sex organs. Since the pistillate and staminate flowers differ only in the functionality of sex organs and display morphological similarity with each other, there is a remote possibility for pollinator insects to discriminate between the two flower sexes prior to flower visitation. Further, both flower sexes produce minute drops of nectar by nectary disc as reward for the appropriate flower visitors. Therefore, morphological similarity in flower structure, shape, calyx and corolla traits, and production of scent and nectar by both flower sexes facilitate pollinator insects to visit both sexes without any discrimination and transfer pollen from staminate to pistillate flowers with pollination as end result. In *X. granatum* and *X. mekongensis*, the production of pistillate and staminate flowers in the same inflorescence and plant indicates that these species are morphologically hermaphroditic but functionally monoecious and exclusively pollinator-dependent.

Almazol & Cervancia (2013) reported that mature buds of *X. granatum* bloom during 1800-2200 h and the flowers remain open until 1000 h on the next day. The present study reports that the mature buds of *X. granatum* and *X. mekongensis* bloom during 1600-1830 h. Individual plants produce pistillate and staminate flowers daily either on the same or different inflorescences and simultaneous presence of both flower sexes does not preclude geitonogamy but facilitates the promotion of out-crossing as the longevity of pollen viability and stigma receptivity is extended until the evening of the next day. In both species, hand pollination tests showed that both geitonogamy and xenogamy are functional with highest fruit set in the latter mode. However, the fruit set rates indicate that individual plants have unknown inherent regulatory mechanism to optimize fruit set rate to enable the inflorescence to hold the growing fruits until maturation and seed dispersal because of their heavy weight. This is very clearly substantiated by low fruit set rates recorded in open-pollination mode and also by the production of 1-3 fruits per inflorescence. The delicate nature of inflorescences also does not enable to hold several heavy mature fruits. Further, such low fruit set rates could be attributable to the production of a few pistillate flowers per inflorescence and/or plant. Low fruit set in open-pollinations is also reported by Almazol & Cervancia (2013). Sporadic flowering in *X. granatum* and *X. mekongensis* appears to be an evolved strategy to produce additional fruits to compensate the low fruit set that results from the seasonal flowering.

Tomlinson (1986) speculated that bees are probably the main pollinators of *Xylocarpus* species. Because, bees easily insert their mouth parts between the stigmatic disc and the stamen tube to collect nectar produced by the ovary disc. Venkatesan (2011) noted that *X. granatum* pollen is collected by honey bees. Almazol & Cervancia (2013) reported that *X. granatum* is a moth flower and principally pollinated by nectar collecting nocturnal moths and supplemented by pollen collecting flies. Bees such as such as *Xylocopa* sp., *Apis dorsata* and *A. cerana* also visit this species; the first two species due to their large size have the difficulty to probe the flower because cup-like structure of corolla and the location of anthers act as barrier for them to make entry into the flower either to collect pollen or nectar. However, *A. cerana* being small in size penetrates into the interior of the corolla tube to collect pollen and pollinates the flowers of *X. granatum*. The present study reports that both *X. granatum* and *X. mekongensis* with simultaneous flowering, and similar floral architecture and morphology attract the same species of flower foragers to their flowers. In both species, hawk moths being the first flower visitors after anthesis and again during dawn hours on the next day act as principal pollinators during nectar collection from both staminate and pistillate flowers. Since they do not land on the flowers to probe the flowers, they minimize time duration at each flower and also fly swiftly collecting nectar from as many flowers as they could in a single visit to the plant. Further, they fly quickly from plant to plant in quest of nectar promoting out-crossing. Butterflies also collect nectar from the flowers of both species after landing but they collect nectar slowly compared to hawk moths and use these flowers as nectar source during forenoon period only. Their flower visits effect both geitonogamous and xenogamous pollination but they serve as supplementary pollinators. Bee foragers including large and small-sized ones collect only pollen from the anthers located in the notches of corolla mouth because the space between corolla mouth and the edge of discoid stigma is very narrow and facilitates only those insects that collect nectar by using long proboscides. Bees tend to stay mostly on the same plant due to their pollen collection activity and hence contribute mostly to geitonogamy although they effect xenogamy in their inter-plant foraging activity throughout the day with a few flower visits from noon and until the time of the occurrence of anthesis on that day. Apart from acting as pollinators, the bees load pollen into the pollen basket or corbicula located on the tibia of the hind legs which consist of hairs and carry them to their hives or nest sites. Such a foraging behavior by bees negatively impacts the pollen availability for the occurrence of pollination. This study shows that hawk moths qualify as principal pollinators while butterflies and bees as supplementary pollinators in both *X. granatum* and *X. mekongensis*. Therefore, these two species are not constrained by a dependence on a specific pollinating agent and the spectrum of pollinators is broad so that they can use different pollinator classes for pollination.

The present study reports that both *X. granatum* and *X. mekongensis* with almost synchronous flowering and common insect pollinator fauna are most likely to receive pollen from each other by their stigmas. Since the pollen grains of both plant species are identical in morphology, they could not be distinguished in pollen recovered from the bodies of pollinator insects. Each of these plant species is likely to experience stigma clogging by the pollen of other species and such a situation could reduce the chances for the pollination by the compatible pollen. Further, there is also a possibility for cross-pollination between *X. granatum* and *X. mekongensis* if inter-specific pollen is compatible for both of them.

Duke et al. (1998) reported that insects attack and kill a substantial number of seeds and propagules of hard seed capsules of *Xylocarpus* which are protected from certain crabs. Allen et al. (2003) reported that crabs act as seed predators and leaf herbivores as seedling predators of *X. granatum*. These authors also stated that although crabs attack seeds, the tough seed coat and high fiber content of seed slow down the seed predation rate. The present study has not found seed or seedling predation by insects or crabs indicating that these animals might be relying on other abundantly available seed or seedling sources in the mangrove forest.

Bhat & Murali (2001) reported that ripening of fruits takes place in a single peak before monsoon season in tropical moist forests because the survival of seeds and seedlings is critically dependent on moisture availability. Chapman (1976) noted that mangroves do not rely absolutely on rainfall for survival because they can extract fresh water from the sea through salt excreting glands. Since most of the propagules and seeds of mangroves directly fall into the river systems or marshy ground below, the moisture need may be met from there. It is in this context, it is important to state that *X. granatum* is an important species because it withstands varying soil conditions, high level of salinity, and lack of freshwater inflow for considerable periods of time and pollution of varying forms (Scholander et al., 1955). Further, Das & Jena (2008) also stated that this species with intertidal location has developed a number of morphological and physiological adaptations to cope with the salt water from the ocean and live within specific zones in its ecosystem. The present study also indicates that the production of a bulk seed set occurs during rainy season, especially in October when estuarine water is properly mixed with fresh water as well as sea water. This state of water salinity is ideal for seed germination and seedling production by both *X. granatum* and *X. mekongensis*.

Jugale et al. (2009) reported that *Xylocarpus granatum* is a critically endangered species of Maharashtra, India. It is disappearing from many locations and currently represented by a few individuals with low genetic variation. Raju (2003) reported that *X. granatum* is represented by several individuals while *X. mekongensis* is represented by a few individuals in the study area. The present study also reports that such a situation still exists and there is a need to take measures for the restoration of populations of these species apart from protecting the surviving individuals.

CONCLUSIONS

Xylocarpus granatum and *X. mekongensis* are semi-evergreen tree species displaying phenological events sequentially. They are morphologically bisexual but functionally unisexual, monoecious and display mixed mating system involving geitonogamy and xenogamy. In both species, hawk moths are principal pollinators while butterflies and bees are supplementary pollinators. Despite possessing functional mixed mating system, these species produce low fruit set which could be due to unknown inherent regulatory mechanisms, delicate inflorescence and the production of a few pistillate flowers at plant level. Therefore, the surviving trees of both the species need to be protected in order to use them to restore their populations.

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