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Reproductive ecology of *Syzygium cumini* (Myrtaceae)

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Abstract
Reproductive ecology of *Syzygium cumini* (Myrtaceae).— *Syzygium cumini* is an evergreen hermaphroditic tree species. The floral characteristics such as creamy white flowers, scent production, copious nectar secretion in exposed cup-shaped calyx, and exposed stamens and stigma due to detachment of corolla following anthesis constitute a generalist pollination syndrome. Accordingly, bees, ants, flies, butterflies and diurnal hawkmoths visit the flowers during day time to collect pollen and/or nectar during which pollination occurs. Among the insects visiting the flowers, diurnal hawkmoths promote cross-pollination and the others, autogamy and geitonogamy. The nectar and pollen produced by the flowers provide certain essential and non-essential amino acids, and protein; the nectar additional provides hexose-rich sugars. The flowers are long-lived and produce fresh nectar each day, and the foragers are accordingly rewarded. Fruits are 1-seeded, pulpy and dispersed by birds; they are collected by local people for self-consumption or for selling in the local markets due to their edible nature.

Key words: generalist pollination syndrome; nectar; ornithochory; pollen; reproductive system.

Resumen
Ecología reproductiva de *Syzygium cumini* (*Myrtaceae*).— *Syzygium cumini* es un árbol hermafrodita de hoja perenne. Sus características florales como flores de color blanco cremoso, producción de aroma, abundante secreción de néctar en el cáliz expuesto en forma de copa, y estambres y estigma expuestos debido al desprendimiento de la corola después de la antesis constituyen un síndrome de polinización generalista. En consecuencia, abejas, hormigas, moscas, mariposas y polillas diurnas visitan las flores durante el día para recolectar polen y/o néctar, durante el cual se produce la polinización. Entre los insectos que visitan las flores, las polillas diurnas promueven la polinización cruzada y los demás, la autogamia y la geitonogamia. El néctar y el polen producidos por las flores aportan ciertos aminoácidos esenciales y no esenciales, y proteínas; el néctar proporciona además azúcares ricos en hexosas. Las flores son longevas y producen néctar fresco cada día, lo que recompensa a los recolectores. Los frutos tienen una semilla, son pulposos y los pájaros los dispersan; son recolectados por la población local para el autoconsumo o para venderlos en los mercados locales debido a su naturaleza comestible.

Palabras clave: néctar; ornitocoria; polen; síndrome de polinización generalista; sistema reproductor.

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INTRODUCTION

Myrtaceae family has a wide distribution in tropical and warm temperate parts of the world. The genus *Syzygium* with about 1100 species is native to the tropical and subtropical regions of the world, particularly to tropical America and Australia. The highest levels of diversity are from Malaysia to northeastern Australia where many species are poorly known and also many more do not have even taxonomic descriptions (Wrigley & Fagg, 2003). The characteristics such as the production of axillary or lateral polychasial cymes, caduceus petals and independent cotyledons in fruits are important to differentiate this genus from other genera of the family (Akoègninou *et al.*, 2006). In India, the genus *Syzygium* is reported to have 75 species but the species list is not available (Anonymous, 1956). Most of the species are valuable as sources of timber, edible fruits, and in traditional medicine (Chadha, 1976). Reddy & Reddy (2008) documented that *S. alternifolium* (Wight) Walp. is an endemic and globally endangered species as per the criteria of IUCN but it is not yet included in IUCN list. *Syzygium cumini* (L.) Skeels is believed to be a native of India or West Indies but it is cultivated in many tropical countries for its timber and fleshy edible fruit (Krishnamurthy *et al.*, 1997; Singh *et al.*, 2019).

Myrtaceae members do not have specialized pollination systems and attract a wide range of vertebrate and invertebrate floral visitors (Eldridge, 1970; Carpenter, 1976; Hopper, 1980; Hopper & Moran, 1981). In *Syzygium* genus, self-compatibility and self-incompatibility systems occur but the first one is more common (Sanewski, 2010). Insect pollination is reported in *S. paniculatum* Gaertn. (Payne, 1991; 1997), *S. syzygioides* (Miq.) Merr. & L. M. Perry (Cox *et al.*, 1992), *S. dealatum* (Burkill) A. C. Sm., *S. effusum* (A. Gray) Müll. Berol. (Webb & Solek, 1996), *S. floribundum* F. Muell. (Crome & Irvine, 1986; Williams & Adam, 2010), *S. pycnanthum* Merr. & L. M. Perry, *S. myrtifolium* Walp. (Mudiana & Ariyanti 2010; 2021), *S. heyneanum* (Duthie) Wall. ex Gamble, *S. travancoricum* Gamble (Ganesh, 1996; Kuriakose *et al.*, 2018*a*), and *S. myhendrae* (Bedd. ex Brandis) Gamble (Pillai & Sreekala, 2021). Ambophily involving insect-pollination and wind-pollination is reported in *S. alternifolium* (Solomon Raju *et al.*, 2014; Badou *et al.*, 2020), *S. caryophyllatum* Alston (Geethika & Sabu, 2017). *Syzygium mamillatum* Bosser & J. Guého is reported to be ornithophilous (Kaiser *et al.*, 2008). Honeyeaters and hawkmoths act as pollinators in *S. tierneyanum* (F. Muell.) T. G. Hartley & L. M. Perry, blossom bats, honeyeaters, and insects in *S. sayeri* (F. Muell.) B. Hyland, insects, birds and blossom bats in *S. cormiflorum* (Crome & Irvine, 1986; Williams & Adam, 2010). *Syzygium laetum* (Buch.-Ham.) Gandhi is pollinated by wind, *S. mundagam* (Bourd.) Chithra by bats, birds and wind (Ganesh, 1996; Kuriakose *et al.*, 2018*a*) and *S. occidentale* (Bourd.) Gandhi by bees, ants and birds (Kuriakose *et al.*, 2018*b*).

In India, *S. cumini* is reported to be adapted for anemophily and entomophily in Lucknow, Uttar Pradesh (Bajpai *et al.,* 2012). In Andhra Pradesh, *S. cumini* is reported to be displaying chiropterophilous pollination syndrome but actually it is pollinated by nocturnal, crepuscular and diurnal insects (Reddi & Rangaiah, 1999). Further, these authors stated that insect-pollination is ineffective and, as a result, this tree species has developed adaptations for anemophily. With this backdrop, the present study is aimed at investigating the floral morphology, floral biology and breeding systems in relation to the foraging activities of insect species and their role in effecting pollination in *S. cumini.* Further, the fruiting behavior and seed dispersal modes in *S. cumini* have also been observed.

MATERIALS AND METHODS

Flowering season and floral biology

Syzygium cumini trees growing in Visakhapatnam (17° 43' 51.744" N, and 83° 20' 16.368" E), Andhra Pradesh, India, were used for the present study during April–August 2022. Field observations were made to record flowering period, floral biology, foraging activity and pollination, breeding systems, and fruiting and seed dispersal aspects. Thirty flowers from 10 trees were collected to describe morphological aspects of flowers briefly, because of reports of inconsistencies on these aspects in the literature.

Fifty mature buds tagged on 10 trees were followed for recording the timing of anthesis and anther dehiscence. A 10X hand lens was used to confirm the dehiscence time and mode. Stigma receptivity was observed by using H_2O_2 test described in Dafni *et al.* (2005). In this test, the period of release of bubbles from the stigma surface following application of H_2O_2 was recorded as the total duration of stigma receptivity during flower life.

Nectar analysis

The presence of nectar was determined by gently pulling a flower from its calyx and firmly pressing its base against a hard surface. Twenty mature buds from five trees which were about to open were bagged before sunrise and removed on the evening of the same day to measure total nectar produced by each flower by inserting a micropipette into the flower base. Again, the flowers were bagged and removed on the next day for measuring the nectar in each flower. The same process was followed on the 3rd and 4th day. The flowers did not produce nectar in the 5th day. The average volume of nectar produced by all these flowers for four consecutive days was taken as the total volume of nectar/flower and expressed in µl. The nectar produced in these flowers was used for measuring nectar sugar concentration each day and then for calculating the mean sugar concentration. A hand sugar refractometer (Erma, Japan) was used for measuring nectar sugar concentration.

Nectar analysis for sugar types was carried out using the paper chromatography method described in Dafni *et al.* (2005). The sugar content/flower is expressed as the product of nectar volume and sugar concentration per unit volume according to Dafni *et al*. (2005). The protocols given in Sadasivam & Manickam (1997) were followed for the quantitative estimation of sucrose, glucose and fructose in mg/flower. The caloric reward of nectar/flower/day was measured as per the formula given in Heinrich (1975). Baker & Baker (1982) method was used for the calculation and classification of sugar ratios of nectar. Paper chromatography method described in Dafni *et al.* (2005) was followed for identifying the amino acid types present in the nectar. Nectar was spotted on Whatman No. 1 filter paper along with the standard samples of 21 amino acids. The paper was run ascendingly in chromatography chamber for 24 h with a solvent system of n-butanol-acetic acid-water in 4:1:5 ratios. The chromatogram was detected with 0.2% ninhydrin reagent and dried at 85°C in an electric oven for 15 min for the development of spots from the nectar and the standard amino acids. The developed nectar spots were compared with those of the standard amino acids to record the amino acid types present in the nectar. Lowry *et al.* (1951) method was used for measuring protein content in the nectar; 40 bagged fresh nectariferous flowers were used.

Pollen output

Twenty mature but undehisced anthers were collected from different trees and placed in a Petri dish. Later, each time a single anther from each flower was taken out and placed on a clean microscope slide and dabbed with a needle in a drop of lactophenol-aniline blue. The pollen mass was drawn into a band and the total number of pollen grains was counted under a compound microscope. Based on these counts, the mean number of pollen grains produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers in the flower for obtaining the mean number of pollen grains per flower. Another set of 10 dehisced anthers was collected in a Petri dish and the pollen grains removed from these anthers were examined under microscope for recording the pollen grain features.

Pollen analysis

The protocols described by Mondal *et al.* (2009) were followed for identifying amino acid types present in the pollen. Pollen was collected from mature anthers and filtered through sieving using meshes of different size (100, 200 and 300 µm) to remove the debris. Then, the pollen was rapidly dried over silica gel at 30°C and stored. Free amino acids were extracted from the pollen using the method described in Mondal *et al*. (2009). Later, the extract thus obtained was used for the qualitative analysis of the free amino acids of pollen using thin layer chromatography. The protocol described

in Sadasivam & Manickam (1997) was followed for the extraction of protein from the pollen samples using phosphate buffer of pH 7.4 and then Lowry *et al*. (1951) protocol was followed for estimating the protein content in the sample.

Foraging behavior and pollination

The insects visiting the flowers were observed during 05:00–19:00 h to record foraging activity period of each insect species. The foraging schedule, forage collected and the flower probing behavior of each insect species were recorded. The number of foraging visits made by each insect species was recorded for 15 min at each hour during the entire length of the observation period to examine the pattern of foraging activity according to the availability levels of nectar and pollen. This field observation on foraging activity of insect species was repeated on four clear sunny days and the data thus collected were used to calculate the average number of visits made by each species at each hour of the day and the percentage of foraging visits by each category of insect species to record the foraging rate of individual insect species and each insect category. The foraging behavior of each insect species was observed with reference to its approach, landing, probing behavior employed for pollen collection and contact with essential organs in effecting pollination.

Breeding systems and fruit set in open-pollinations

Breeding systems were tested for different modes of self- and cross-pollination. Spontaneous autogamy was tested by bagging five complete inflorescences consisting of 210 flowers on the same tree. Fifty mature buds were bagged, opened the next day after the occurrence of anthesis, anther dehiscence and stigma receptivity; the stigma was pollinated with the pollen of the same flower using a brush and bagged again to test hand self-pollination. Eighty mature buds were bagged after emasculation, opened the next day after the commencement of stigma receptivity; the stigma was pollinated with the fresh pollen of a different flower of the same tree using a brush and bagged again to test geitonogamy. Sixty mature buds were bagged after emasculation, opened the next day after the occurrence of stigma receptivity; the stigma was pollinated with the fresh pollen from the flowers of a different tree using a brush and bagged again to test xenogamy. The bagged flowers were followed for 30 days for fruit set. Based on the flowers that produced fruits, the percentage of fruit set was calculated. Twenty inflorescences with 840 flowers from 10 trees were tagged prior to anthesis and followed for natural fruit set. The percentage of fruit set was calculated based on the number of fruited flowers. Fruits are characteristically 1-seeded and hence seed set rate was treated as equal to fruit set rate.

Fruit and seed characters and seed dispersal

Fruit and seed characters were described in view of the reports of inconsistencies in these characters. Field observations were made on fruit dispersal agents and the role of them was briefly described.

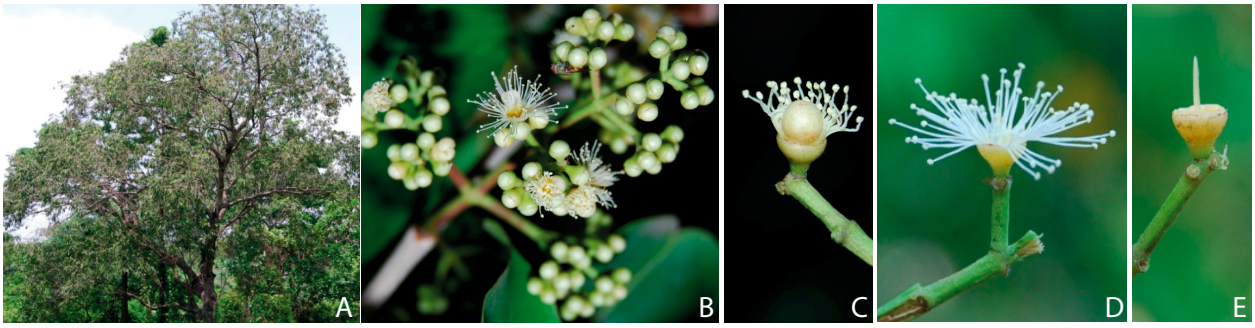

Figure 1. Morphological aspects of *Syzygium cumini*: (A), habit; (B), inflorescence with mature buds and flowers; (C), individual flower at anthesis; (D), individual flower; (E), stigma.

RESULTS

Flowering phenology and flower morphology

Syzygium cumini is a tropical evergreen tree species which grows wild in many wild pockets in Simhachalam, Adavarivaram, Anandapuram, Madhurawada and Rushikonda in Visakhapatnam (Fig. 1A). It is also planted and cultivated for its edible fruits and ornamental value. The flowering occurs *en masse* during May–July. The inflorescences are intercalary polychasial cymes each with an average of 46 ± 8.9 flowers; they are borne at the end of each branch (Fig. 1B, C). The pattern of flowering in each cyme is that the central flower matures first while the lateral ones flower subsequently. The flowers are small, 4 mm diameter, creamy white, mildly odoriferous, bisexual and actinomorphic (Fig. 1D). The calyx consists of five creamy white sepals, united with thalamus and form a cup-like structure. The corolla consists of five petals, free, creamy white, delicate and inserted on the top of a deep cup-like receptacle. The petals form a cap in the bud condition and fall off as a calyptra due to the pressure of the growing stamens inside. The stamens are 46–50, arranged on the rim of the receptacle in several whorls. They are bent inwards in bud condition; straighten at the time of opening and extend outwards after anthesis. They are creamy white and tipped with versatile anthers. The ovary is bicarpellary syncarpous with 18–22 ovules on axile placentation. The style is terminal, 10–11 mm long and terminates into a simple stigma (Fig. 1E).

Floral biology

The flowers are open throughout the day with peak anthesis during 18:00–20:00 h. The buds while opening push the corolla cap upwards exposing the stamens and stigma. The petals soon fall off. At this stage, the stamens bend downward and gradually stretch out completely exposing the stamens. The anthers dehisce by longitudinal slits following anthesis. The pollen output per anther is 201 ± 17. The pollen grains are white, triangular, powdery and 15.75 × 18 × 13.5 µm in size. The style arises from the center of the cup, and shows growth after anthesis. The stigma attains receptivity 24 hours after anthesis and remains receptive until the evening of 4th day of flower life. The nectar secretion occurs continuously for a period of four days from the time of anthesis. A flower produces 3.71 ± 1.0 µl of nectar consisting of 43.1 ± 5.26% sugar concentration; the total sugar content per flower is 1.904 mg. The nectar energy per flower is 26.767 joules. The sugar types in the nectar include sucrose, glucose and fructose; their quantity per flower varies with sugar type. The sucrose is 0.22 mg, glucose 0.233 mg and fructose 0.224 mg. The nectar is hexose-rich and the sugar ratio is 0.481. The pollen analysis for amino acids showed that it has four essential and six non-essential amino acids for insects. The essential ones include arginine, histidine, isoleucine and lysine while the non-essentials include aspartic acid, cysteine, cystine, glycine, hydroxyproline and serine (Table 1). The total protein content per 1 mg of pollen is 0.15 mg. The nectar contains six each essential and non-essential amino acids for insects. The essential amino acids are arginine, histidine, lysine, phenylalanine, threonine and tryptophan. The non-essential amino acids include aspartic acid, cysteine, cystine, glycine, serine and tyrosine (Table 1). The protein content in the nectar is 0.213 mg/flower. The flowers fall off at the end of 5th day.

Foraging activity of insects and pollination

The flowers were foraged by bees, ants, flies, butterflies and diurnal hawkmoths (Table 2). The data collected on the foraging visits of all these groups of insects showed that butterflies made 53%, bees 28%, flies 9% and ants and hawkmoths, each 5% of total visits paid to flowers (Fig. 2). The bees were *Apis dorsata* Fabricius, 1793 (Fig. 3A, B), *A. cerana* Fabricius, 1793 (Fig. 3C), *A. florea* Fabricius, 1793 (Fig. 3D) and *Trigona iridipennis* Smith, 1854 (Fig. 3E) (Apidae) and *Halictus* sp. (Halictidae) (Fig. 3F). The ants represented only one species, *Camponotus* sp. (Formicidae) (Fig. 3G). The flies were *Helophilus* sp. (Syrphidae) (Fig. 3H) and *Chrysomya megacephala* (Fabricius, 1794) (Calliphoridae) (Fig. 3I). The butterflies included 18 species representing Papilionidae, Pieridae, Nymphalidae, Lycaenidae and Hesperiidae families. The Papilionidae and Pieridae each was represented by two

Table 1. Essential and non-essential amino acids present in the pollen and nectar of *Syzygium cumini.*

Amino acid type	Essential amino acids		Amino acid type	Non-essential amino acids	
	Pollen	Nectar		Pollen	Nectar
Arginine	+	+	Alanine	-	-
Histidine	+	+	Amino butyric acid	-	-
Isoleucine	+	-	Aspartic acid	+	+
Leucine	-	-	Cysteine	+	+
Lysine	+	+	Cystine	+	+
Methionine	-	-	Glutamic acid	-	-
Phenylalanine	-	+	Glycine	+	+
Threonine	-	+	Hydroxyproline	+	-
Tryptophan	-	+	Proline	-	-
Valine	-	-	Serine	+	+
			Tyrosine	-	+

+ = Present; - = Absent

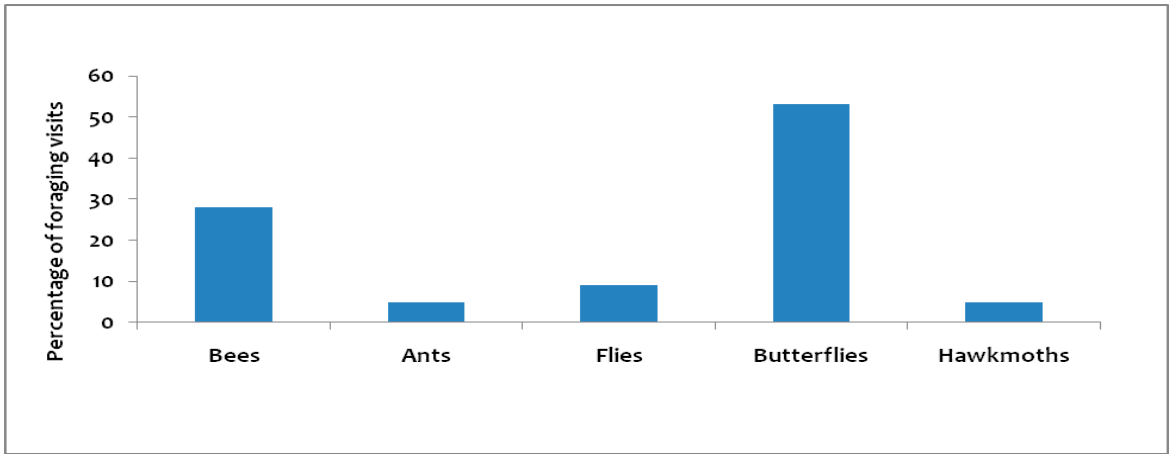

Figure 2. Percentage of foraging visits of different groups of insects on *Syzygium cumini*.

species, Nymphalidae 10 species, Lycaenidae three species and Hesperiidae one species. The Papilionids were *Pachliopta aristolochiae* (Fabricius, 1775) and *P. hector* (Linnaeus, 1758). The Pierids were *Catopsilia pomona* (Fabricius, 1775) and *C. pyranthe* (Linnaeus, 1758). The Nymphalids were *Hypolimnas bolina* (Linnaeus, 1758), *Tirumala limniace* (Cramer, 1775), *T. septentrionis* (Butler, 1874) (Fig. 3J), *Parantica aglea* (Stoll, 1782) (Fig. 3K), *Danaus chrysippus* (Linnaeus, 1758) (Fig. 3L), *D. genutia* (Cramer, 1779) (Fig. 3M), *Precis iphita* Cramer, 1782 (Fig. 3N), *Euploea core* (Cramer, 1780) (Fig. 3O), *Melanitis leda* Linnaeus, 1758 and *Acraea violae* Fabricius, 1775. The Lycaenids were *Castalius rosimon* (Fabricius, 1775), *Everes lacturnus* Fruhstorfer, 1924 (Fig. 3P) and *Jamides celeno* (Cramer, 1775). The Hesperiid was *Hasora chromus* (Cramer, 1780) (Fig. 3Q). The diurnal hawkmoths belonged to Sphingidae and they were *Macroglossum gyrans* Walker, 1856 and *Cephonodes hylas* Linnaeus, 1771 (Sphingidae) (Fig. 3R). Further, one unidentified nocturnal moth species (Fig. 3S) had also occasionally collected nectar after sunset for a brief period.

Table 2. List of insect foragers recorded on *Sygyzium cumini*.

Order/Family	Insect species	Forage sought
Hymenoptera		
Apidae	*Apis dorsata* F.	N + P
	Apis cerana F.	N + P
	Apis florea F.	N + P
	Trigona iridipennis Smith	N + P
Halictidae	*Halictus* sp.	N + P
Formicidae	*Camponotus* sp.	N
Diptera		
Syrphidae	*Helophilus* sp.	N
Calliphoridae	*Chrysomya megacephala* F.	N
Lepidoptera		
Papilionidae	*Pachliopta aristolochiae* L.	N
	Pachliopta hector L.	N
Pieridae	*Catopsilia pomona* F.	N
	Catopsilia pyranthe L.	N
Nymphalidae	*Melanitis leda* L.	N
	Acraea violae F.	N
	Precis iphita Cr.	N
	Hypolimnas bolina L.	N
	Tirumala limniace Cr.	N
	Tirumala septentrionis Butler.	N
	Parantica aglea Stoll.	N
	Danaus chrysippus L.	N
	Danaus genutia Cr.	N
	Euploea core Cr.	N
Lycaenidae	*Castalius rosimon* F.	N
	Everes lacturnus Godart	N
	Jamides celeno Cr.	N
Hesperiidae	*Hasora chromus* Cr.	N
Sphingidae	*Macroglossum gyrans* Walker	N
	Cephonodes hylas L.	N

N = Nectar, P = Pollen

The bees, flies and ants collected forage regularly from 07:00/08:00 to 17:00 h with peak activity at 11:00–13:00 h (Fig. 4). All butterflies collected nectar from 08:00 to 17:00 h with peak activity at 10:00–12:00/13:00 h (Figs. 5–7). Hawkmoths collected nectar from 06:00 to 08:00 h and again from 16:00 to 19:00 h (Fig. 8). The cup-shaped calyx with exposed nectar facilitated all insect foragers to collect nectar with great ease. The flowers with copious amount of nectar presented in numerous polychasial cymes at each branch level enabled butterflies to remain on the same tree for a long time and such a foraging activity was considered to be promoting geitonogamy. While collecting nectar, the insects came in contact with both the stigma and stamens invariably ensuring the transfer of pollen

Figure 3. Floral visitors of *Syzygium cumini*: (A–B), *Apis dorsata*; (C), *Apis cerana*; (D), *Apis florea*; (E), *Trigona iridipennis*; (F), *Halictus* sp.; (G), *Camponotus* sp.; (H), *Helophilus* sp.; (I), *Chrysomya megacephala*; (J), *Tirumala septentrionis*; (K), *Parantica aglea*; (L), *Danaus chrysippus*; (M), *Danaus genutia;* (N), *Precis iphita*; (O), *Euploea core*; (P), *Everes lacturnus*; (Q), *Hasora chromus*; (R), *Cephonodes hylas*; (S), unidentified nocturnal moth.

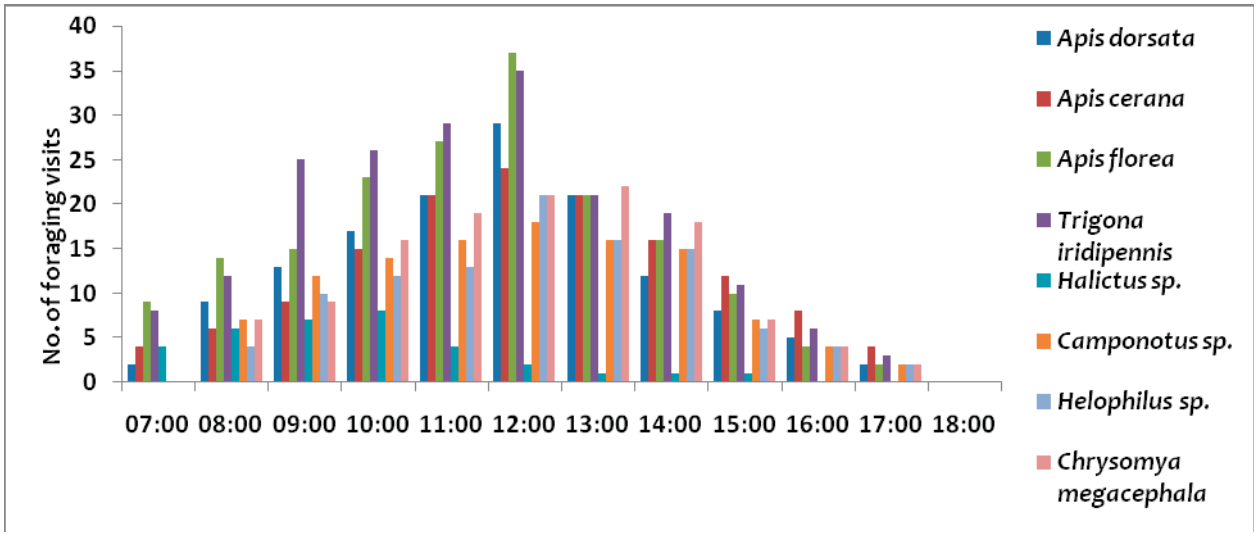

Figure 4. Hourly foraging activity of bees, ants and flies on *Syzygium cumini*.

and pollination of stigmas. Among all insects, only bees collected pollen along with nectar in the same or in another foraging visit. Since the bees were involved in pollen collection, they tended to stay mostly on the same flower/polychasial cyme or on the same tree and such a foraging activity appeared

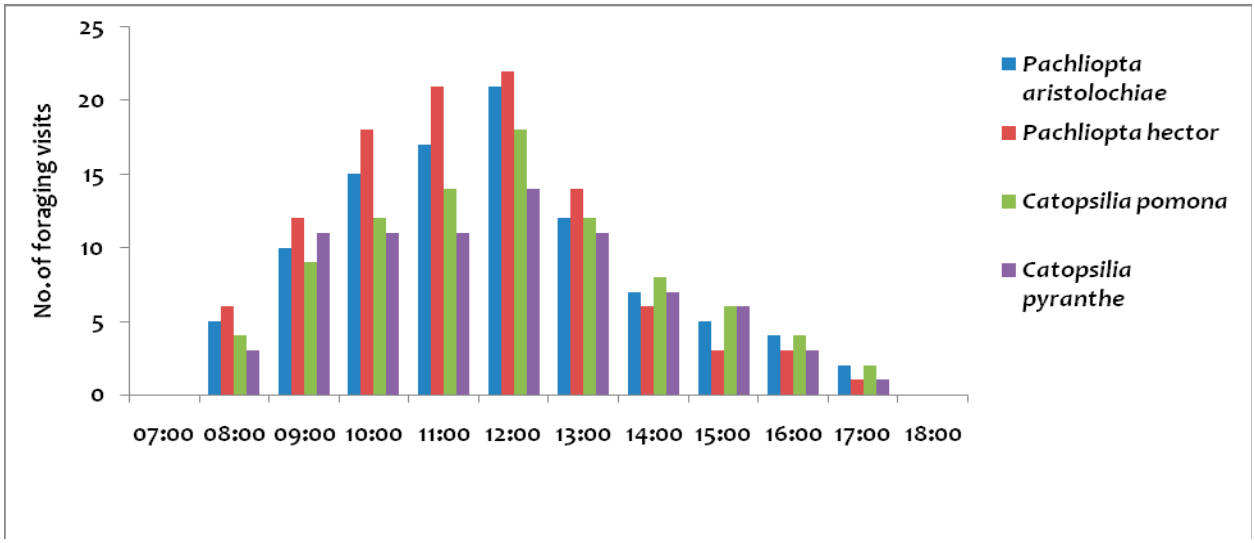

Figure 5. Hourly foraging activity of papilionid and pierid butterflies on *Syzygium cumini*.

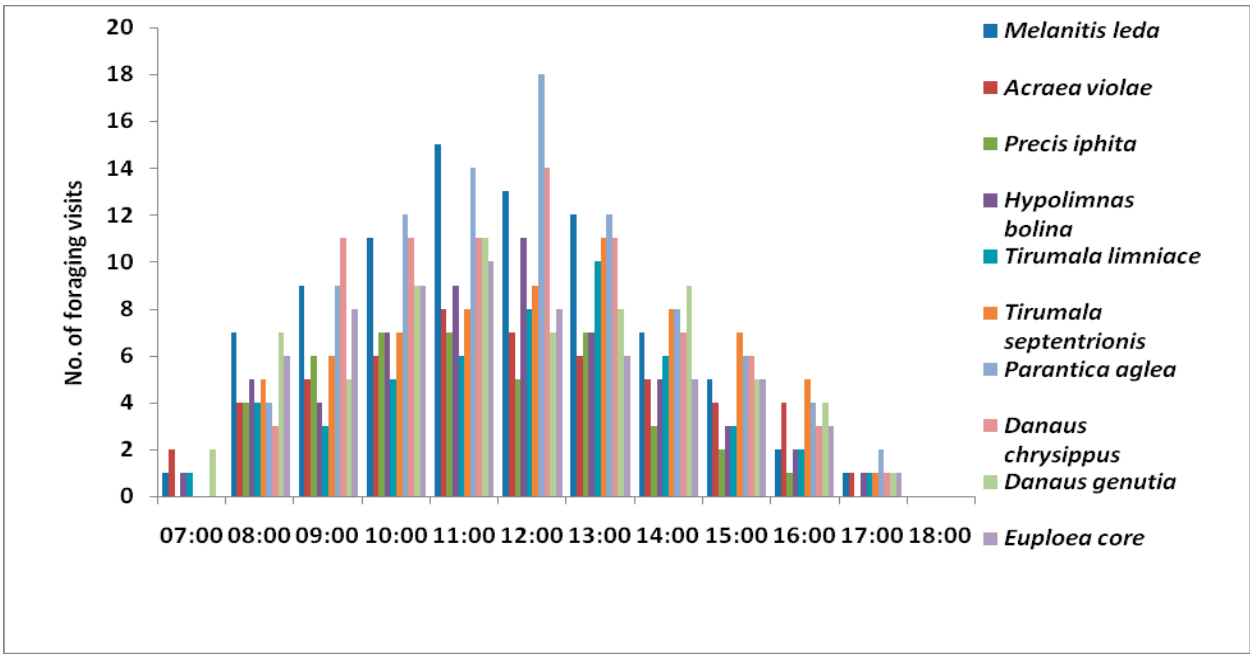

Figure 6. Hourly foraging activity of nymphalid butterflies on *Syzygium cumini*.

to be effecting mostly geitonogamy rather than xenogamy. The sole ant species being a resident forager was also found to be effecting mostly or exclusively geitonogamy. Flies, butterflies, the diurnal hawkmoths and the moth being exclusive nectar foragers tended to fly swiftly between flowers of the same or conspecific trees growing nearby effecting both geitonogamy and xenogamy. The possibility for the occurrence of vector-mediated autogamy is almost ruled out due to non-receptive nature of stigma on the day of anthesis and the falling of stamens on the morning of the 2nd day of anthesis.

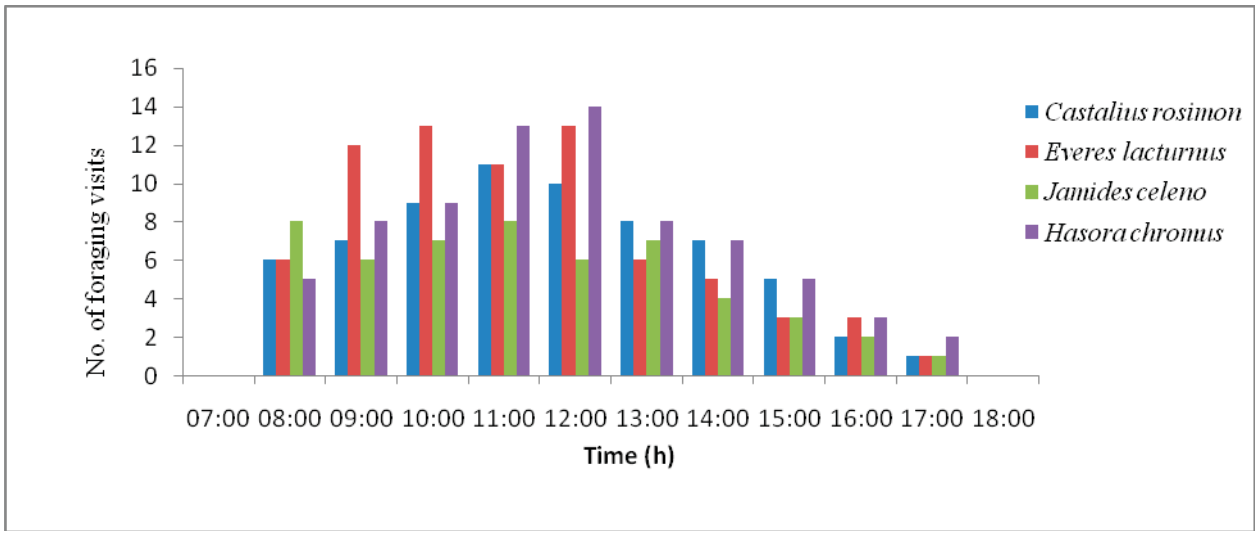

Figure 7. Hourly foraging activity of lycaenid and hesperiid butterflies on *Syzygium cumini*.

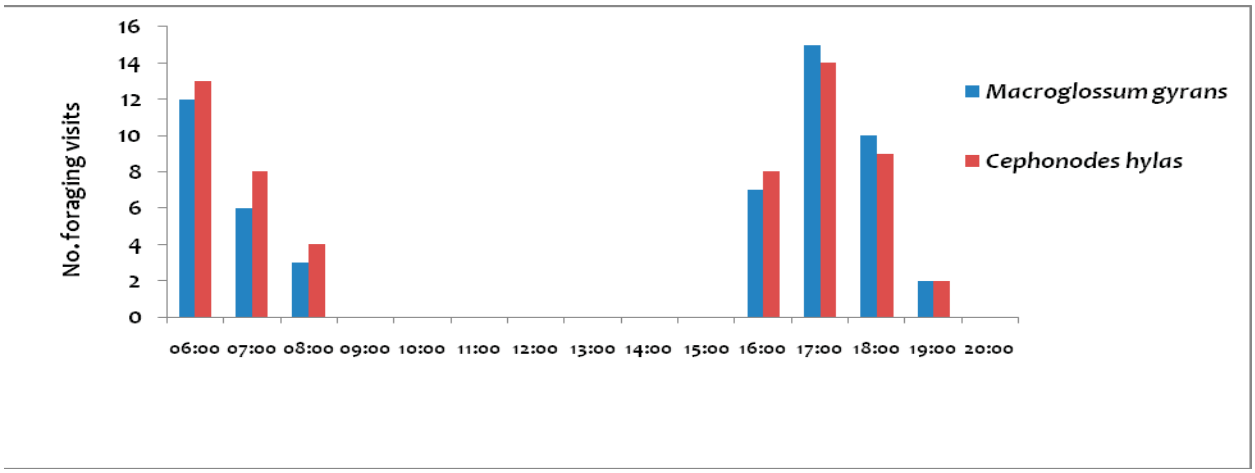

Figure 8. Hourly foraging activity of diurnal hawkmoths on *Syzygium cumini*.

Breeding systems, natural fruit set and seed dispersal

Hand-pollination tests showed that the flowers set fruit through autogamy, geitonogamy and xenogamy. Individual flowers that were bagged did not produce any fruits but fruit set was 8% when entire inflorescences were bagged. Fruit set was 8% in manipulated autogamy, 46% in geitonogamy, 78% in xenogamy and 51% in open-pollinated flowers (Table 3). The fruits mature within 3–5 weeks and drop off during July–August. The ripe fruit is a globose dark purplish one stony-seeded berry with fleshy, sweet, juicy and slightly acidic taste pulp; it shows different colors from green to light purple to dark purple during its growth and development (Fig. 9A–D). Local people collect fruits due to their edible and commercial value and probably contribute to seed dispersal. Frugivorous birds such as *Pycnonotus cafer* (Linnaeus, 1766),

Table 3. Results of breeding systems in *Syzygium cumini.*

Treatment	Number of flowers bagged/tagged/ pollinated	Number of fruits produced	Fruit set (%)
Autogamy (individual flowers bagged)	50	0	0
Autogamy (5 complete inflorescences about to initiate flowering bagged)	210	16	8
Autogamy (manual pollination, bagged)	50	4	8
Geitonogamy (manual pollination, bagged)	80	37	46
Xenogamy (manual pollination, bagged)	60	47	78
Open-pollination (20 inflorescences)	840	427	51

Figure 9. Fruits of *Syzygium cumini*: (A–D), different stages of fruit development.

P. jocosus (Linnaeus, 1758), *Iole indica* (Jerdon, 1839) (Passeriformes: Pycnonotidae), *Acridotheres tristis* (Linnaeus, 1766) (Passeriformes: Sturnidae), *Zosterops palpebrosus* (Temminck, 1824) (Passeriformes: Zosteropidae), *Megalaima viridis* (Boddaert, 1783) and *Megalaima haemacephala* (Müller, 1776) (Piciformes: Megalaimidae) were found feeding on the fruits occasionally. These birds fed on the fruit pulp either by spitting out and leaving the seed attached to the parent tree. In seed-spitting mode, the birds carried the fruit with their beak to other trees of the area, landed on the branch and fed on the pulp and dropped the seed under the tree. In seed-leaving mode, the birds simply ate the pulpy part without removing the fruit from the parent tree. In both modes, birds dispersed seeds either under the parent tree or in the vicinity of the parent tree or in distant areas. The ripe fruits that were not collected by locals remained on the ground under the tree canopy. Fruit dispersal occurs through feeding of fleshy part of the fruits by birds opportunistically and by humans until fruit stock is exhausted.

DISCUSSION

In this study, the transition period from dry period (May) to the most humid period (June/July) of the year corresponds to the initiation of blooming in *Syzygium cumini*. The massive blooming period for this species coincides with the gradual increase in rainfall. The humid period in June/July is also characterized by a decrease in temperature and long daylight hours. Fidalgo & Kleinert (2009) reported that the beginning of transition to the most humid period of the year corresponds to the beginning of blooming in Myrtaceae members in Brazil and the most intense flowering period coincides with the progressive increase in rainfall, as the studied

plant. Other authors who also carried out studies in Brazil on this aspect showed that Myrtaceae blooming follows abrupt increases in humidity levels which occur during the transition from the dry to rainy season (Kawasaki, 1989; Proença & Gibbs, 1994; Silva & Pinheiro, 2007). Temperature or day length or both are the main factors that contribute to flowering in any species (Beardsell *et al.*, 1993). Flowering peaks tend to occur during the period of the year with the longest daylight hours in the Neotropics and Paleotropics (Schaik *et al.*, 1993).

Hansman (2001) stated that plants pollinated by generalist insects would tend to bloom in the humid or wet season when a greater abundance of insects would occur. Fidalgo & Kleinert (2009) reported that Myrtaceae species in Brazil bloom when humidity, temperature and day length increase progressively and these species then are visited by generalist insects. In this study, *S. cumini* shows an increase in flowering intensity with an increase in humidity and day length and a decrease in temperature.

Different authors reported that *Syzygium* species do not have specialized pollination systems and, as a result, they attract a wide range of vertebrate and invertebrate flower visitors (Carpenter, 1976; Hopper, 1980; Hopper & Moran, 1981). Pollinators involving either vertebrates or invertebrates or both have been reported in different *Syzygium* species as mentioned in the Introduction section.

In India, Bajpai *et al*. (2012) reported that *S. cumini* is adapted for wind and insect pollination. Reddi & Rangaiah (1999) noted that *S. cumini* is a self-compatible mass bloomer which presents new flowers daily at late evening time. The present study also shows that *S. cumini* is a mass bloomer presenting polychasial cymes at the end of branches in order to be quite distinct against the foliage to attract flower foragers. The cymes produce flowers daily day-long with high density during late evening time. The tree is functionally highly self-compatible as fruit set occurs through manipulated and un-manipulated autogamy and geitonogamy; but the flowers with male phase on the day of anthesis and female phase on successive days of flower life prevent the occurrence of autogamy and facilitate geitonogamy only due to long flower-life. The tree is also cross-compatible as fruit set rate is the highest in xenogamy mode. Reddi & Rangaiah (1999) described that *S. cumini* is pollinated by nocturnal moths and day-active insects such as bees, wasps, ants, beetles, bugs, moths and butterflies. In this study, the floral characteristics such as creamy white flowers, scent production, copious nectar secretion in cup-shaped calyx, exposed stamens and stigma due to detachment of corolla following anthesis in *S. cumini* indicate the function of a generalist pollination syndrome and, accordingly, the tree also attracts a variety of day-active bees, ants, flies, butterflies and hawkmoths. Of these insects, hawkmoths as swift fliers making inter-tree visits frequently proved to be important for cross-pollination, while all other insects by making visits mostly on the same tree proved to be important for geitonogamy. Its flowers never received foraging visits by nocturnal foragers despite the availability of new flowers due to peak anthesis at late evening period. The absence of nocturnal foragers such as moths and bats could be relatable to the simultaneous occurrence of attractive and rewarding floral resources elsewhere (Bolten & Feinsinger, 1978). The generalist pollination syndrome evidenced in *S. cumini* has also been reported in other studied species of *Syzygium*; this syndrome would enable the tree to achieve both cross- and self-pollination to set high fruit set rate (Hopper & Moran, 1981; Crome & Irvine, 1986; Webb & Solek, 1996; Mudiana & Ariyanti, 2010). Despite the function of mixed breeding system, this tree is able to set fruit only 51% in open-pollinations. This rate of fruit set in open-pollinations could be attributable to non-occurrence of self- or cross-pollination in many flowers, selective abortion of self-fertilized ovules and nutrient-deficiency in the habitat of the *S. cumini*.

Several studies suggest that sucrose-rich nectars are preferred by hummingbirds, long-tongued bees, Old World bats, moths, and butterflies, whereas hexose-rich nectars are preferred by perching birds, short-tongued bees, New World bats, and flies (Baker & Baker, 1983, 1990; Perret *et al*., 2001; Dupont *et al*., 2004). Bees prefer nectars of high concentrations (Baker & Baker, 1975; Heinrich, 1979). The present study found that *S. cumini* flowers with hexose-rich nectar with high sugar concentration attract different groups of insects. Individual flowers with high energy yielding nec-

tar are energetically rewarding for the visiting insects for four consecutive days due to continuous production of nectar. Further, the nectar and pollen are also sources of certain essential and non-essential amino acids and total protein. Copious pollen production at flower level is another advantage for the tree to attract bee foragers which collect pollen for brood development. The massing blooming at tree level and presentation of flowers as clusters in polychasial cymes are also additional advantages for the foragers to reduce flight time and search time, and display flower constancy; such a state of floral rewards and presentation of flowers is highly economical for the foragers (Law, 1992; Grant, 1996). However, it is disadvantageous to maximize self-pollination within and between flowers of the same tree. Therefore, *S. cumini* with massive blooming pattern, peculiar floral structural and functional characters, and mixed breeding system is able to produce fruits mostly through self-pollination, particularly functional through geitonogamy and supplemented by cross-pollination.

Badou *et al*. (2020) reported that the plant species of Myrtaceae usually produce more ovules in the ovary but a few succeed in fertilization to produce seed. In *S. guineense* (Willd.) DC. subsp. *macrocarpum* (Engl.) F. White, only one seed is produced per fruit while the other ovules become aborted. Different authors experimentally demonstrated that in *S. cumini* the indole compounds present predominantly in dominant seeds inhibit resource uptake by the sub-ordinate seeds and in effect each fruit produces only one seed (Khan *et al.*, 1995; Arathi *et al.*, 1996; Kader *et al*., 2000). Krishnamurthy *et al*. (1997) reported that in *S. cumini*, seed abortion could also result from the production of death chemicals by the dominant ovules that kill other ovules of the same flower. These reports indicate that the production of 1-seeded fruits is a function of either the predominance of indole compounds in dominant seeds that inhibit resource uptake by the sub-ordinate seeds or the production of death chemicals by the dominant ovules that kill other ovules in the same flower. The present study indicates that *S. cumini* invariably produces 1-seeded fruits irrespective of the number of ovules produced by each fruited flower. Further, the study also found that there is no initiation of seed production from more than one ovule in any fertilized flower, suggesting that ovule abortion event permitting only one fertilized ovule to proceed with the production of fruit/seed is genetically regulated by the production of chemicals that cause ovule abortion.

Pillai & Sreekala (2021) reported that *S. myhendrae* fruits are consumed by birds and bonnet monkeys but their role in fruit dispersal is not documented. Sinu *et al.* (2012) reported that *S. cumini* fruits are dispersed by frugivorous birds such as *Pycnonotus jocosus* (Linnaeus, 1758), *Psittacula roseata* (Biswas, 1951), *Megalaima viridis* (Boddaert, 1783), *Zosterops* palpebrosus (Temminck, 1824), *Nectarinia zeylonica* (Linnaeus, 1766), *N. minima* (Sykes, 1832), *Iole indica* (Jerdon, 1839), *Acridotheres tristis* (Linnaeus, 1766) and *Megalaima haemacephala* (Müller, 1776). These birds feed on the pulp of the fruits either by swallowing, spitting out and leaving the seed attached to parent tree. In this study, it is found that some frugivorous bird species such as *Pycnonotus cafer* (Linnaeus, 1766), *P. jocosus* (Linnaeus, 1758)*, Megalaima viridis* (Boddaert, 1783), *Zosterops palpebrosus* (Temminck, 1824), *Iole indica* (Jerdon, 1839), *Acridotheres tristis* (Linnaeus, 1766) and *Megalaima haemacephala* (Müller, 1776) feed on the fruit pulp by using seed spitting out and seed-leaving modes and in this feeding process, they act as seed dispersers either under the parent tree or in the vicinity of the parent or in distant areas. But, these birds use the fruits as food source only occasionally and act as seed dispersal agents. Local people collect fruits for self-consumption or for selling in the local market and, in this activity, humans probably play a role in seed dispersal at parental or non-parental sites.

CONCLUSIONS

Syzygium cumini is a mass blooming evergreen tree species. The flowers are hermaphroditic, strikingly protandrous and self-compatible. The flowers presented in polychasial cymes borne at the end of branches appear quite distinct against the foliage and attract a variety of insect species. The flowers display the function of self-pollination with and without pollinators and cross-pollination mediated exclusively by pollinator insects. The floral features

characterize a generalist pollination syndrome and, accordingly, the flowers are foraged and pollinated by different groups of insects of which diurnal hawkmoths play a role as prime pollinators in effecting cross-pollination while all other insects visiting the flowers effect largely self-pollination. This tree with mixed mating system is able to fruit to the extent of 51% in open-pollinations. The fruit is fleshy and characteristically 1-seeded irrespective of the number of ovules produced by each fruited flower and such a function is attributed to genetic regulation by the production of chemicals that cause ovule abortion. Some frugivorous birds use the fleshy part of fruits as food opportunistically and act as seed dispersers. Local people collect fruits for self-consumption or for selling in the local market and, in this activity, they probably play a role in seed dispersal.

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AUTHORSHIP CONTRIBUTION STATEMENT

Lankapalli Kala Grace: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Palathoti Suvarna Raju:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Aluri Jacob Solomon Raju:** Supervision, Writing – review & editing.

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