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ENTOMOPHILY AND ORNITHOCHORY IN THE INDIAN SANDALWOOD, *SANTALUM ALBUM* L. (SANTALACEAE)

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Abstract: *Santalum album* is an evergreen tree species that flowers twice in a year with a gap of one month during May-September. It is hermaphrodite, obligately self-incompatible and entomophilous. The principal pollinators are bees and nymphalid butterflies while a species of hoverfly and potter wasp are additional pollinators in both flowering seasons. The fruits are fleshy, 1- or 2-seeded drupes and seed dispersal is ornithochorous. The study indicates that *S. album* is obligately vector-dependent for pollination and seed dispersal.

Keywords: Hermaphroditism, self-incompatibility, bees, butterflies, flies, wasps, drupe.

Introduction

Santalum is a genus of hemiparasitic tree species distributed throughout South and South-east Asia, Australia and the Pacific. The heartwoods of several species of this genus are highly valued for their aromatic oil which is widely employed in perfumery, medicines and incense [19]. This genus is assigned with 18 species but only one, *S. album*, has been widely used for various purposes and is the pride of India and labelled as Queen of essential oils [22]. *S. album* is a small aromatic evergreen tree native to tropical pockets of south India and South-east Asia [11]. It is listed as Vulnerable by IUCN due to over-exploitation, habitat degradation and wood smuggling for trade [2, 4, 14]. It is reported as a threatened species in South India [23]. This tree species with distinctive fragrance is treated as sacred in native Indian religions. Its heartwood is very costly and has high commercial value in domestic and international markets due to its rich content of aromatic essential oil, which is used in food products, cosmetics, perfumes, aromatherapy and pharmaceutical industries. Different parts of this tree are used in Ayurveda, Unani and Siddha medicinal systems to cure various diseases in humans [24].

Different authors have documented that *Santalum* species are facultatively allogamous and lacking ability for apomixis or parthenocarpy [17, 18, 27]. *S. album, S. austrocaledonicum* and *S. lanceolatum* do not have reproductive barriers and have high level cross-compatibility between them [19]. In the genus *Santalum*, pollination ecology information is available for *S. album* only, but the information is conflicting with respect to self- or non-self-pollination or the pollinating insects. Prehaten and Ratnaningrum [21] reported that *S. album* is self-compatible and pollinated by flies, bees and butterflies in Gunungkidul, Central Java. Baskorowati [5] reported that *S. album* is predominantly out-crossing and pollinated by insects, predominantly bees and ants in Yogyakarta, Indonesia. In India, different authors reported on the pollinators of *S. album*.

Sindhuveerendra and Sujatha [25] reported that *S. album* flowers are designed for self-pollination, and are self-compatible and pollinated by ants, bees, butterflies and beetles in Bangalore. Jyothi et al. [16] noted that *S. album* is an obligate outcrosser and adapted for pollination by insects in Visakhapatnam. Bhaskar [6] noted that *S. album* is self-incompatible, obligately outcrossing and pollinated by flies and bees. Veerendra and Padmanabha [29] observed that *S. album* is pollinated by insects, with ants and bees regular pollinators in Bangalore. But, the information reported by these authors on the pollination ecology of *S. album* is conflicting with reference to pollination mode and pollinator classes of insects. It is in this context, the present work is aimed at reporting on floral structural and functional aspects, the role of individual categories of pollinating insects, breeding systems, and fruit and seed seed rates in *S. album*.

Materials and Methods

Flowering and floral biology: Ten trees of *Santalum album* growing in the wild patches of Andhra University campus (17°42'N Latitude and 82°18'E Longitude), Visakhapatnam, Andhra Pradesh, India, were selected for study during March-December 2021. Bearing in mind the Vulnerable status of the species, a small number of inflorescences and flowers were selected and used for the study. Ten inflorescences which were about to initiate flowering on five trees were tagged and followed to record the flower-opening schedule and timing and mode of anther dehiscence. Anther dehiscence timing was confirmed by observing the anthers under a 10x hand lens. Twenty-five fresh flowers were used to record the flower type, sex, shape, colour, odour, symmetry, calyx, corolla, stamens, ovary, style and stigma. The floral configuration and rewards presentation aspects were observed in relation to the probing and forage collection activities of insects. Ten un-dehisced mature anthers were collected from five trees and placed in a Petri dish. Later, a single anther was taken out each time and placed on a clean microscope slide (75 x 25 mm) and dabbed with a needle in a drop of lactophenol-aniline blue. The anther tissue was then observed under the microscope for pollen. The pollen mass was drawn into a band, and the total number of pollen grains was counted under a compound microscope (40x objective, 10x eye piece). The same procedure was followed for counting the number of pollen grains in each anther collected. 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. The same pollen grains were examined under the microscope for recording pollen grain features. Thirty ovaries, five each from six trees were examined under the microscope to record the number of ovules per flower. The pollen-ovule ratio was determined by dividing the average of the number of pollen grains per flower by the average number of ovules per flower. The value thus obtained was taken as the pollen-ovule ratio [9]. The stigma receptivity was observed by H_2O_2 testing [10]. In this test, the period of release of bubbles from the surface of the stigma following application of hydrogen peroxide as the duration of stigma receptivity period during flower life. Data on all these aspects were collected during the June and August periods.

Pollinators: Insects foraging at the flowers were observed throughout the day on two clear sunny days in June and again in August for their mode of approach, landing, probing behaviour and contact with the floral sexual organs during the two flowering seasons. One 10-minute count of insect visits to 30 flowering inflorescences of two closely spaced and profusely flowering trees at each hour throughout the day from 6:00 to 18:00 o'clock was made on two consecutive sunny

days in each flowering season. The number of flowers visited by each insect species in a 10-minute period at each hour was recorded to know the flower visiting rate with the time of day, and the relative percentage of foraging visits made by each insect category was calculated by pooling all foraging visits made by individual species of each insect category.

Breeding system and seed dispersal: Breeding systems were assessed based on the results of hand-pollination tests. Fifty flowers from five inflorescences from five trees were bagged without hand-pollination for spontaneous autogamy. One hundred flowers from 40 inflorescences from five trees were emasculated; of these, 50 flowers were manually pollinated with the pollen of the same flowers for artificial autogamy while another 50 flowers were manually pollinated with the pollen of other flowers of the same tree for geitonogamy. In all these three pollination modes, the flowers did not set any fruit and hence these details are not presented in a tabular form. A further 50 inflorescences, consisting of 578 flowers from five trees during the May-June flowering season, and another 50 inflorescences, consisting of 624 flowers from five trees during the August-September flowering season, were tagged and exposed to open cross-pollination by pollinating insects. The fruit set and seed set rates recorded in both flowering seasons are presented in Table 1. Casual field observations were made to record frugivores and their role in seed dispersal.

Table 1: List of insect pollinators on *Santalum album*

Order/Family	Insect species	Forage sought	Total No. of foraging visits/day	
			May-June	August-September
Hymenoptera				
Apidae	*Apis dorsata* F.	Pollen + Nectar	152	157
	Apis cerana F.	Pollen + Nectar	137	141
	Apis florea F.	Pollen + Nectar	124	124
Vespidae	*Eumenes conica* F.	Nectar	58	60
Diptera				
Syrphidae	*Helophilus* sp.	Nectar	38	41
Lepidoptera				
Nymphalidae	*Euploea core* Cramer	Nectar	36	40
	Hypolimnas misippus L.	Nectar	45	47
	Junonia lemonias L.	Nectar	34	39
	Phalanta phalantha Drury	Nectar	34	37
	Danaus chrysippus L.	Nectar	39	43
Total foraging visits/day			**697**	**729**

Results

Flowering and floral biology: *Santalum album* is an evergreen tree species. Leaves are petiolate, simple, elliptic to ovate, base and apex acute, glabrous and upper surface shiny. The flowering occurs twice a year during May-June and August-September; the flowering was moderate in the former flowering season and very intense in the latter flowering season. Floral buds are borne in axillary and terminal paniculate cymes (Fig. 1a, b). They are light green to light yellowish but are purplish-brown at anthesis, which occurs daylong from 6:30 to 18:00 o'clock, with pronounced anthesis during the forenoon period. The flowers are pedicellate, small, purplish-brown, unscented, hermaphroditic, and actinomorphic (Fig. 1c). The perianth is green to whitish-

cream, sepaloid, connate basally into a campanulate tube and apically expanded into 5 minutely ciliate tepals. The floral disc consists of 4 bright maroon-coloured scales giving a false appearance of petals; they are alternate with the perianth-lobes. The stamens are usually 4 and rarely 5, hairy, free, alternated with disc scales and exserted with 2-celled basifixed anthers dehiscing by longitudinal slits at anthesis. Individual anthers produce 1432 ± 57 (Mean ± S.D) pollen grains. The pollen grains are monads, tri-colpate and verrucate in the region of inter-colpium (Fig.1d). The ovary is globose and 1-celled with 1 ovule, rarely 2, which are pendulous from below the long central column (Fig. 1e–g). The ratio of 1- and 2-ovuled flowers is 5:1. The style is simple with a 3-lobed stigma which attains receptivity to pollen about an hour after anthesis and continues for about 2 days of flower-life. The mean pollen-ovule ratio varies with the number of stamens and ovules per flower. This ratio is 5,728:1 in 4-stamened and 1-ovuled flowers, 7,160:1 in 5-stamened and 1-ovuled flowers, 2,864:1 in 4-stamened and 2-ovuled flowers, and 3,580:1 in 5-stamened and 2-ovuled flowers. Individual flowers secrete nectar in trace amounts only and it is easily accessible due to short-tubed and well-exposed perianth base.

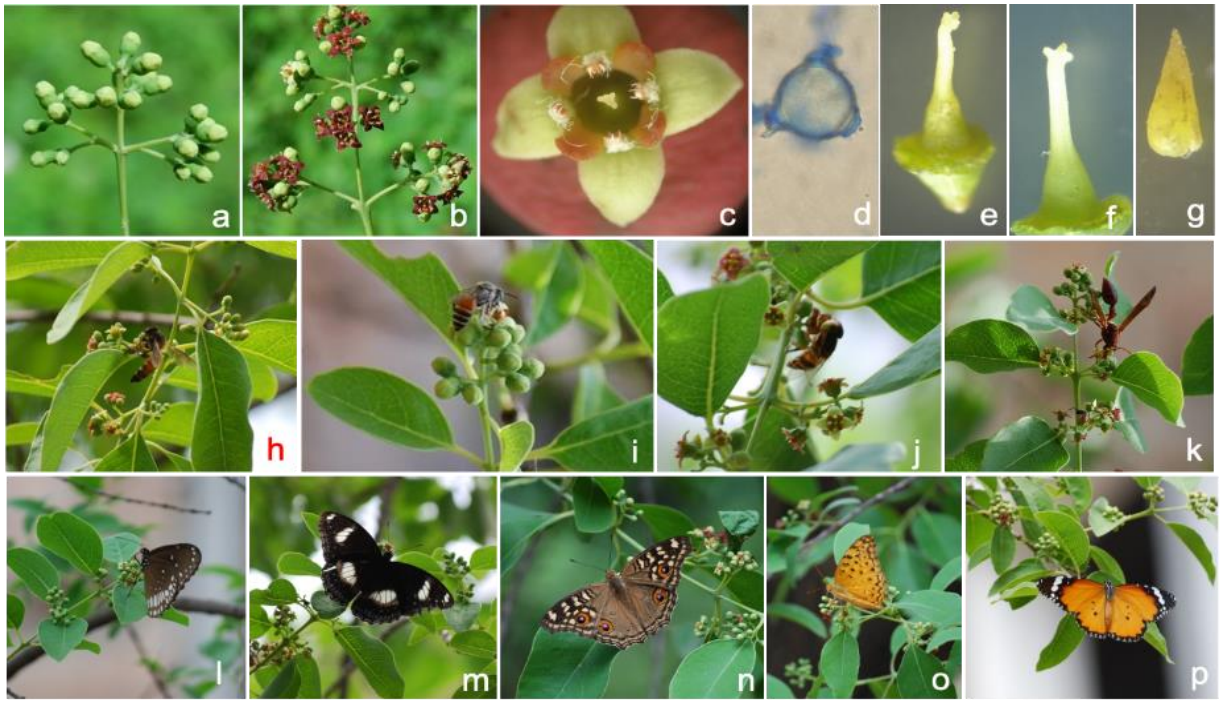

Fig. 1: *Santalum album*: a. Buds, b. Inflorescence in flowering phase, c. Flower, d. Pollen grain, e & f. Pistil, g. Ovary, h. *Apis dorsata* collecting nectar, i. *Apis florea* collecting nectar, j. *Helophilus* sp. collecting nectar, k. *Eumenes conica* collecting nectar, l-p. Nymphalid butterflies collecting nectar – l. *Euploea core*, m. *Hypolimnas misippus*, n. *Junonia lemonias*, o. *Phalanta phalantha*, p. *Danaus chrysippus*. Photocredit: Prof. Aluri Jacob Solomon Raju

Pollination: Anthesis occurs throughout the day but more mature buds are open during the forenoon period. The flowers are slightly protandrous, indicating the function of weak dichogamy but are strikingly herkogamous due to clear cut spatial separation of stamens and 3-lobed stigma; both sex organs are almost placed at the same height during flower-life. Herkogamous condition does not facilitate the occurrence spontaneous pollination and vector-mediated self-pollination on the same tree despite the maturation of both male and female sex organs nearly synchronous. The

flowers with nectar and pollen offering as rewards attracted different insect species which included honey-bees, a hover fly species, a potter wasp species, and nymphalid butterflies (Table 1). The honey-bees included *Apis dorsata* F. (Fig. 1h), *A. cerana* F. and *A. florea* F. (Fig. 1i). The hover fly was *Helophilus* sp. (Fig. 1j) while the potter wasp was *Eumenes conica* F. (Fig. 1k). The nymphalid butterflies were *Euploea core* Cramer (Fig. 1l), *Hypolimnas misippus* L. (Fig. 1m), *Junonia lemonias* L. (Fig. 1n), *Phalanta phalantha* Drury (Fig. 1o) and *Danaus chrysippus* L. (Fig. 1p). Of these, honey-bees and butterflies were regular foragers and visited the flowers throughout the day with pronounced activity during forenoon period in both flowering seasons (Fig. 2, 3). The fly and the wasp were occasional foragers only in both flowering seasons. The honey-bees made 60%, butterflies 27%, hover fly 8% and the potter wasp 5% of total foraging visits during the May-June flowering season. The corresponding percentages of foraging visits made by these insects during the August-September flowering season were 58%, 28%, 8% and 6% respectively (Fig. 4). The data showed similar pattern of insect visiting activity between two flowering seasons. The honey-bees landed in an upright position on the perianth lobes and probed the flowers for nectar with great ease and also collected pollen from the anthers which are situated opposite to the rim of the perianth lobes in the same visit. Sometimes, they collected either pollen or nectar in the same visit. They were voracious pollen collectors due to which they spent more time at each flower and also on the same tree. Since anthesis rate is high during the forenoon period, these bees spent more time (2-4 minutes) at each flower/panicle for collecting both floral rewards while they spent less time (1-3 minutes) at each flower/panicle during the afternoon period as the anthesis rate was less and accordingly the availability of fresh flowers is minimal. As a consequence, the bees mostly confined to the same flowering tree during the forenoon period while they made frequent flower visits to different flowering trees during afternoon period. The hover fly and the wasp species as occasional foragers landed in an upright position on the nearby flowers and probed the targeted flowers for nectar collection. Since nectar was produced in traces in each flower, these two species quickly departed from the probing flowers and visited many flowers on the same and also on other simultaneously flowering trees in quest of more nectar reward. The butterflies also displayed the foraging behavior exhibited by the fly and the wasp to collect nectar by inserting their proboscis to the flower base with great ease. They made frequent flower visits on different flowering trees to collect the required levels of nectar. The foraging behavior exhibited by all these insects indicated that honey-bees effect cross-pollination mainly during afternoon period while butterflies with their frequent inter-tree foraging trips effect cross-pollination throughout the day. The fly and the wasp species also effect cross-pollination but they act as additional pollinators only due to their occasional foraging activity. The flowers were never visited by nocturnal insects in either flowering season.

Breeding system and seed dispersal: Hand-pollination tests conducted for obligatory self-pollination, manipulated self-pollination (geitonogamy) and out-crossing (emasculated flowers) by pollinating agents showed that obligatory and manipulated selfing modes are not functional as there was absolutely no fruit and seed set in both flowering seasons. Only 13% and 20% of the emasculated flowers exposed to pollinators in nature set fruits during the May-June and August-September flowering season, respectively. In both flowering seasons, the seed set is 100% in all fruited flowers (Table 2). Seed number recorded in fruited flowers is indicative of seed production also from 2nd ovule in 2-ovuled flowers. Fruits mature in about 3 months. The fruit is a globose blackish-purple 1-seeded succulent drupe. Seed dispersal is mediated by birds which eat

the outer fleshy pericarp. Casual observations indicated that some passerine bird species used the fruits as food source; these included *Acridotheres tristis* L., *Sturnus pagodarum* Gmelin (Sturnidae), *Pycnonotus cafer* L., *P. jocosus* L. (Pycnonotidae) and *Argya caudata* Dumont (Leiothrichidae). The birds held fruits with their beak and proceeded to another tree species for eating the fleshy part conveniently and in this process they either dropped the seeds without swallowing them or excreted them undamaged when swallowed. Therefore, the birds acted as seed dispersal agents.

Table 2: Fruit and seed set in out-crossing mediated by pollinating agents in nature in *Santalum album*

Flowering season	No. of flowers tagged	No. of flowers set fruit	Fruit set (%)	No. of seeds produced in all flowers that set fruit	Seed set (%)
May-June	578	25	4.3	27*	100
August-September	624	58	9.2	63*	100

*Number in excess of total flowers that set fruit indicates seed production from 2-ovuled flowers.

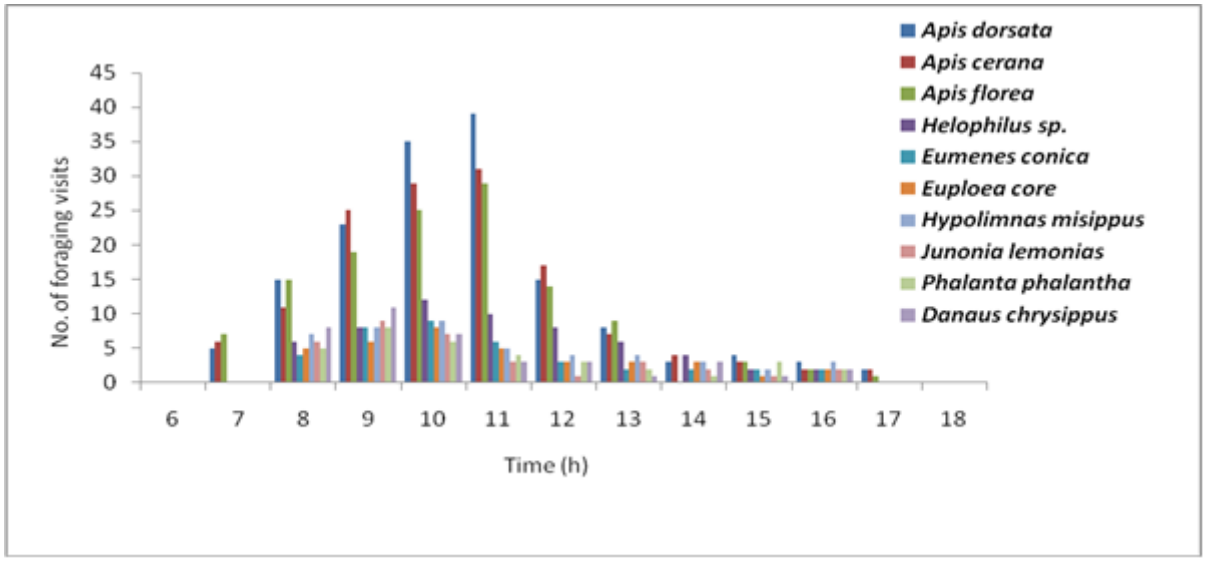

Fig. 2: Hourly foraging activity of insects on *Santalum album* during May-June flowering season

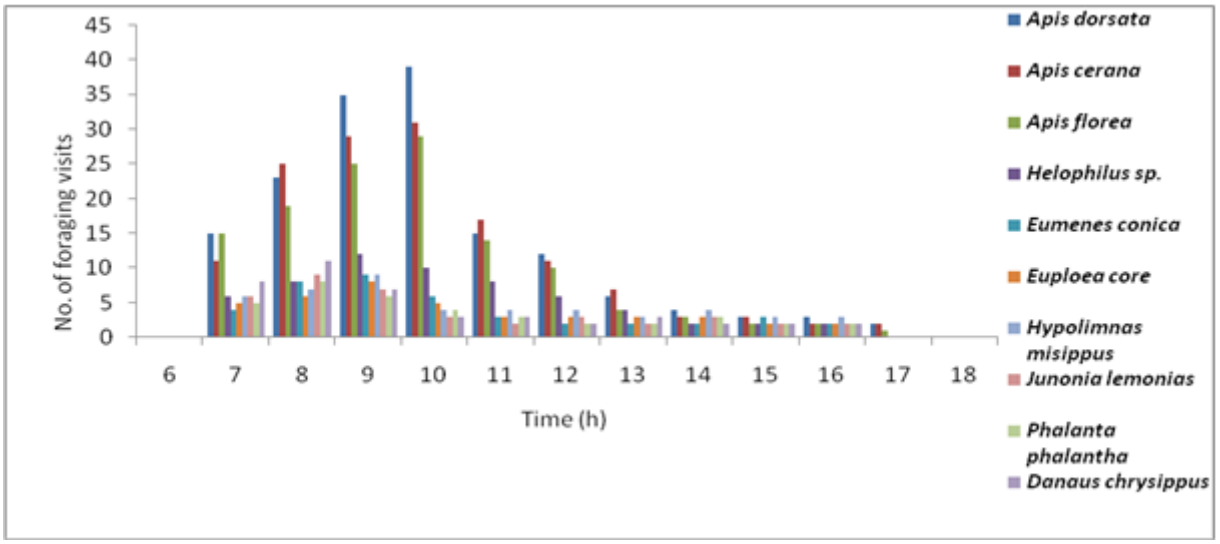

Fig. 3: Hourly foraging activity of insects on *Santalum album* during August-September flowering season

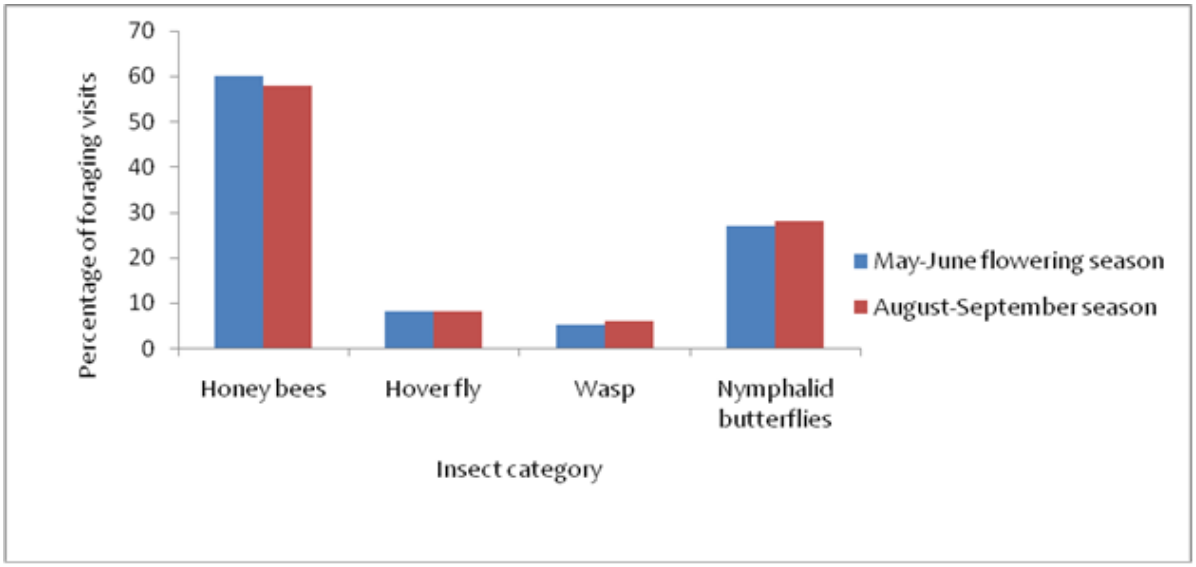

Fig. 4: Percentage of foraging visits on *Santalum album* during May-June and August-September flowering seasons

Discussion

Various authors have reported the flowering season of *Santalum album* differently in Indonesia and India. In Indonesia, its flowering occurs during June-October [12, 20], May-June and December-January [5]. In India, flowering occurs during February-July [8], July-September with sparse flowering outside this period [26], once (September-December) or twice (March-May and September-December) [1], and three times in a year (May-June, August-September and November-February) [16]. Bhaskaran et al. [7] reported that *S. album* flowers once a year in its initial years of flowering and twice a year in later years during March and September. But, the regular flowering of twice in a year is rare in the same trees. The present study observed that *S. album* flowers twice in a year in the same trees but there is variation in flowering intensity, with moderate level during May-June period and very intense level during August-September period. Such a variation is attributable to low moisture and high temperature during the former period and high moisture and low to moderate temperature during the latter period. The flowering twice a year appears to be genetically functional in combination with the local meteorological conditions and soil nutrient environment.

Veerendra and Padmanabha [29] reported that *S. album* produces three types of flowers on different trees: the flowers displaying the stigma above the anthers (pin), the flowering displaying the stigma below the anthers (thrum) and the flowers displaying the stigma and anthers at the same level. The production rate of these 3 types of flowers varies from tree to tree in a population. In the present study, *S. album* trees are found to produce only one type of flower, in which both stigma and anthers are placed almost at the same level throughout the flower lifespan. Furthermore, both sex organs are spatially separated, the placement of which completely prevents the occurrence of spontaneous self-pollination.

The breeding system in *S. album* is reported by different authors. This tree species is self-incompatible and an obligate out-crosser [6, 16], predominantly out-crossing with variation in self-incompatibility level in individual trees [5], self-compatible and self-pollinating [21] and

facultatively allogamous with variation in self-incompatibility levels in individual trees and lacking ability for apomixes or parthenocarpy [17, 18, 27]. The variation in self-incompatibility rate is advantageous for the tree as it facilitates the function of self-compatibility for the occurrence of self-pollination [28]. The present study showed that *S. album* is self-incompatible and obligately cross-pollinating as there is no fruit or seed set in self-pollination modes.

Jyothi et al. [16] noted that *S. album* is obligately entomophilous. Bhasker [6] reported that *S. album* is entomophilous, with pollination commonly effected by flies (*Phytomia argyrocephala, Eristalinus arvorum* and *Dolichomerus crassa*) and bees (*Apis florea, A. cerana* and *A. dorsata*). Sindhuveerendra and Sujatha [25] reported that *S. album* is pollinated by ants, bees, butterflies and beetles. Veerendra and Padmanabha [29] reported that *S. album* is pollinated by insects, with ants and bees as regular pollinators. Prehaten and Ratnaningrum [21] reported that *S. album* is pollinated by flies, bees and butterflies. Baskorowati [5] reported that *S. album* is pollinated by insects, predominantly by bees and ants. The present study also found *S. album* to be entomophilous, and the pollinating insects are honey-bees, a hoverfly, a potter wasp and nymphalid butterflies. Of these, honey-bees effect cross-pollination mostly during afternoon period due to their tendency to remain on the same tree for pollen and nectar collection from fresh flowers while nymphalids effect cross-pollination throughout the day through frequent inter-tree foraging visits due to availability of traces of nectar from individual flowers. The hoverfly and the potter wasp also effect cross-pollination with their frequent inter-tree foraging visits throughout the day but they act as additional pollinators due to their occasional foraging activity. The low fruit set rates in both flowering seasons could be partially attributed to voracious pollen collection activity of honey bees and low cross-pollination rate. The high fruit set rate recorded during the August-September flowering season is relatable to nutrient-rich soil environment due to the occurrence of rains. Each fruit invariably produces a single seed from 1-ovuled flowers but 2 seeds from 2-ovuled flowers. But, it is not known whether all 2-ovuled flowers produce 2 seeds if both ovules are fertilized.

Howe [13] reported that in *S. album*, soft, edible and nutritious tissues of fleshy fruits are a primary food source for birds and mammals. Jordano [15] noted that the birds and mammals spit out or drop through defecation the undamaged seeds of *S. album* away from the parental trees. Balasubramanian and Santhoshkumar [3] noted that Indian Grey Hornbill, *Ocyceros birostris* is a seed dispersal agent for *S. album* in Sathyamangalam Forest Division, Tamil Nadu. Balasubramanian et al. [4] reported *Pycnonotus* spp., *Sturnus pagodarum, Acridotheres tristis, Eudynamys scolopacea, Turdoides affinis* and *Phaenicophaeus viridirostris* act as frugivores-cum-seed dispersers of *S. album* in Anaikatty Hills, Western Ghats. The present study observed that certain passerine birds such as *Acridotheres tristis, Sturnus pagodarum, Pycnonotus cafer, P. jocosus* and *Argya caudata* are involved in the seed dispersal of *S. album*. Therefore, *S. album* is ornithochorous.

Conclusions

Santalum album is an evergreen tree species which flowers twice a year, with a gap of one month, during May-September. Its flowers are bisexual, nectariferous, weakly protandrous, obligately self-incompatible and entomophilous. The pollinators include bees, nymphalid butterflies, a hoverfly and a potter wasp, of which the first two categories are principle and consistent pollinators while the others are additional pollinators due to their occasional foraging

activity in both flowering seasons. The fruits are fleshy, 1- or 2-seeded drupes and seed dispersal is mediated exclusively by birds. Therefore, *S. album* is obligately vector-dependent for pollination and seed dispersal.

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ENTOMOFILIE ȘI ORNITOCHORIE LA ARBORELE DE SANTAL INDIAN, *SANTALUM ALBUM* L. (SANTALACEAE)

(Rezumat)

Santalum album este o specie sempervirescentă de arbore ce înflorește de două ori pe an, mai puțin în intervalul mai-septembrie. Este o specie hermafrodită, cu autopolenizare și entomofilă. Principalii polenizatori, în ambele perioade de înflorire, sunt albinele și fluturii (nimfalide), iar mușteleș și viespii sunt polenizatori suplimentari. Fructele sunt drupe cărnoase cu 1-2 semințe, iar răspândirea semințelor se face prin ornitocorie. Studiul de față subliniază faptul că *S. album* este o specie obligat dependentă de vectori pentru polenizare și răspândirea semințelor.

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