



An ecological study of vegetative and sexual modes of reproduction in oligohaline mangrove associate plant species, *Dalbergia spinosa* Roxb. (Fabaceae), *Solanum trilobatum* L. (Solanaceae), *Typha domingensis* Pers. (Typhaceae), *Saccharum spontaneum* L. and *Myriostachya wightiana* (Nees ex Steud.) Hook.f. (Poaceae)

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ABSTRACT

Five mangrove associate plant species, *Dalbergia spinosa*, *Solanum trilobatum*, *Typha domingensis*, *Saccharum spontaneum* and *Myriostachya wightiana*, growing in oligohaline zone of Coringa Mangrove Forest, Andhra Pradesh, India, were studied for their vegetative and modes of reproduction. *T. domingensis* is monoecious while all other species are hermaphroditic. Explosive pollination mechanism is functional in *D. spinosa* while buzz-pollination is functional in *S. trilobatum* but both species are melittophilous. *T. domingensis*, *S. spontaneum* and *M. wightiana* are typical anemophiles. *D. spinosa* is anemochorous and hydrochorous, *S. trilobatum* barochorous and hydrochorous, and the other species are typically hydrochorous. All five plant species are ecologically important to sequester carbon dioxide, check soil erosion, add soil fertility and also useful in traditional medicine. Further, *T. domingensis*, *S. spontaneum* and *M. wightiana* are useful for making thatched houses and handicraft products. Therefore, these plant species need to be properly protected and utilized in a traditional way.

Keywords: Mangrove associates, oligohalines, monoecy, hermaphroditism, explosive pollination mechanism, buzz-pollination, melittophily, anemophily, anemochory, hydrochory, barochory.

1. INTRODUCTION

Mangroves are a fascinating group of plants distributed along tropical and subtropical shorelines. They are subjected to daily saltwater flushing, low oxygen levels at root level, high light and temperature conditions, and periodical and intermittent tropical storms. They have economical, medicinal and environmental values to coastal communities. Mangroves are classified into two groups according to their habitats, true mangroves and mangrove associates. True mangroves are species that specifically grow in intertidal zones, while mangrove associates are species that grow in littoral and terrestrial habitats. Different mangrove species adopt distinct strategies for adaptation to grow in low to high salinity habitats (Lin, 2001; Wang et al. 2003). Mangrove associates are often called as back mangroves or semi-mangroves (Lacerda et al., 2002). They grow along the landward side of estuarine mangrove ecosystems, reduce salinity levels and have enormous capacity to absorb industrial effluents and other forms of pollutants, and sequester carbon dioxide. Further, they act as natural sewage treatment plants and have paramount importance in eco-repair in the in the estuarine ecosystems. Despite their importance in multiple ways, most of the species have not been investigated for their ecology, pollination and mode of reproduction. With this backdrop, the present study was contemplated to provide certain details of ecological aspects of vegetative growth, vegetative and sexual modes of reproduction in five mangrove associate plant species, *Dalbergia spinosa* (Fabaceae), *Solanum trilobatum* (Solanaceae), *Typha domingensis* (Typhaceae), *Saccharum spontaneum* and *Myriostachya wightiana* (Poaceae) with reference to their value in the development of natural green belt along the landward side of the estuarine ecosystem, minimization of soil erosion and reduction in salinity levels.

2. MATERIALS AND METHODS

The Coringa mangrove forest lies between 16°30'–17°00'N and 82°10'–80°23'E in the deltaic region of East Godavari district, Andhra Pradesh, India. Field studies were made on the populations of *Dalbergia spinosa*, *Solanum trilobatum*, *Typha domingensis*, *Saccharum spontaneum* and *Myriostachya wightiana* growing along the landward side of this mangrove forest. Observations on the organization of inflorescences, the spatial positioning of flowers, and their position on the plant were made since these features are important for foragers to effect pollination. The flower longevity was recorded by marking ten just open flowers and following them until they dropped off. Ten marked mature buds were tagged and followed for *D. spinosa* and *S. trilobatum* to record anthesis schedule. The same buds were followed to record the time and mode of anther dehiscence. The floral morphological details were observed under microscope and recorded as these details are important to characterize their pollination syndrome. In case of *D.*

spinosa and *S. trilobatum*, the stigma receptivity was observed by H₂O₂ test as given in Dafni et al. (2005). Ten mature buds were tagged, bagged and followed to measure the volume of nectar secreted by them. Then, the average volume of nectar per flower was recorded and expressed in μ l. Nectar sugar concentration was also simultaneously recorded using a Hand Sugar Refractometer (Erma, Japan).

The insects visiting the flowers of *D. spinosa* and *S. trilobatum* were insects only while other plant species were never visited by insects. These two plant species were observed carefully day long for four days in different weeks during flowering season. The hourly foraging visits of each insect species were recorded on fifty selected inflorescences. The data obtained was used to calculate the percentage of foraging visits made by each insect species per day in order to evaluate their relative importance in pollination. Simultaneously, they were observed for their foraging behavior such as mode of approach, landing, probing behaviour, the type of forage they collected, and contact with essential organs to result in pollination. Fruit maturation period, fruit dehiscence, seed dispersal and establishment were observed in the field.

3. RESULTS

***Dalbergia spinosa* Roxb.**

Dalbergia spinosa is a back mangrove associate and grows well along the backwater creeks extended into landside areas representing oligo haline zone of the mangrove forest. It forms dense patches and closely covers the soil and sunlight penetration through the foliage is a remote possibility (Figure 1a). With its extensive growth along the creeks, it is found to stabilize the banks of creeks and adds organic matter upon death to the estuarine zone. The foliage is quite distinct during rainy season when leaf flushing occurs and gradually foliage withers during winter and eventually sheds during summer season. In summer season, the soil floor occupied by this plant is totally exposed to sunlight and the creek banks also experience erosion.



Figure 1 *Dalbergia spinosa*: a. Habit – left –flowers, b. Fruiting.

The plant is a much-branched glabrous shrub or small tree with twining habitat and tap root system without no aerial roots. The branches are short and end with spines. Leaves are compound, imparipinnate and crowded at nodes of spinous branchlets; leaflets are petiolate, elliptic-ovate with obtuse to emarginate apex. Stem is round, smooth and dark brown. Inflorescence is a few-flowered raceme and borne in the axils of compound leaves. The flowering occurs during February-April. The flowers are small, reniform, white, glabrous, bisexual and zygomorphic. Calyx is campanulate with 5-lobed apex, green, and glabrous. Corolla is papilionaceous with 1 large standard petal (3 mm long and 2.5 mm broad), 2 wing petals (2.5 mm long) and 2 keel petals (2.5 mm long). Stamens are 10 diadelphous with 9 + 1 arrangement; filaments fused to form a short column but anthers are free. The ovary is shuttle-shaped, bicarpellary unilocular syncarpous and contains 1-2 ovules on marginal placentation. The style is 1, terminal, incurved at the tip and extended into a capitate stigma.

Mature buds open early in the morning during 0700-0900 h daily (Figure 1a). Anther dehiscence occurs in mature bud about 30 minutes prior to anthesis while stigma is receptive after anthesis and become unreceptive by the end of the day by which time the flowers close back. The flowers produce minute volume of nectar which varies from 0.7 to 1.2 μ l with a sugar concentration of 25-31%. The flowers fall off on the evening of the 2nd day if not pollinated while the corolla together with stamens and stigma falls off on the 2nd day and the pistil remains in place in pollinated flowers.

The flowers being small and white in color are prominent against foliage but they are usually covered by the foliage and the visits of foragers to flowers and their probing behavior for forage collection could not be made. However, the insect foragers

proceeding towards flowers were observed and accordingly the species were recorded as pollinators. The flowers have explosive pollination mechanism with the keel enclosing the sexual apparatus and escorted by wings after anthesis. With the visit of insects, upon landing on the wing and keel petals, the stigma and staminal column springs out from the keel petals and strikes against the ventral side of the insect effecting pollination. After the explosion of keel petals, the stamens and stigma are exposed until the standard petal closes them back at the end of the day. The insect foragers included honey bees (*Apis cerana*, *A. florea* and *Trigona iridipennis*) and leaf cutter bees (*Megachile* sp.) (Table 1). They foraged during day-light hours from 0800-1600 h with more activity during 11-1300 h for collecting nectar and pollen (Figure 4).

The fruits mature in a time span of 3-4 weeks (Figure 1b). They are initially green and turn brown when mature. Fruit is a reniform, glabrous, 25 mm long and 17 mm broad, 1-seeded pod with one convex margin and the other concave mid-notched one. Fruits are indehiscent, light in weight and disperse by wind from the mother plant and by water when reaches the soil floor.

***Solanum trilobatum* L.**

Solanum trilobatum is a back mangrove associate (Figure 2a). It is a prickly diffuse, much-branched perennial shrub with woody base and flourishes well along the creeks densely covering the soil. It grows well during rainy season and at this time; it produces most of the foliage in perennial plants. Seeds also germinate; produce seedlings and new plants subsequently. The flowering occurs early in plants that come up from underground perennial root system and late in plants that come up from the seeds. The flowering is seasonal occurring during July-October. But, sporadic leaf flushing and flowering also occurs throughout the year in damp habitats saturated with tidal water. Leaves ovate in outline, obtusely 3-5-lobed, glabrous or slightly stellate with a few prickles along the petiole and midrib. Inflorescence is extra-axillary, pedunculate, cymose and 3-8 flowered. Flowers are pedicellate (10-12 mm long), purplish-blue, widely divergent, actinomorphic and bisexual (Figure 2b). Calyx is with narrow teeth, 3 mm long and sparsely stellate. Corolla is deeply lobed, stellate-pubescent outside, purple coloured, 12-15 mm long and reflexed. Stamens are 5, epipetalous, yellow and protruding; the filament is 4 mm long while anther is 8-10 mm long with an apical pore. The pistil has bicarpellary syncarpous globose 2 mm long glabrous ovary with many ovules arranged on axile placentation, extended into a slender 16 mm long style which in turn is extended into a small obscurely bi-lobed stigma.



Figure 2 *Solanum trilobatum*: a. Habit, b. Close-up view of flower, c. *Apis dorsata* collecting nectar, d. *Xylocopa pubescens* collecting nectar, e. Nymphalid butterfly, *Junonia almana*, f. Flowering and fruiting phase.

Mature buds open during morning hours with anther dehiscence taking place at the terminal pore shortly before anthesis. In dehisced anthers, the pollen is kept inside the tubular thecae with small apical opening restricting direct access to pollen by the pollen foragers. The pollen grains are yellow, globose, triangular, trizonocolporate, exine is granulate with prominent operculum.

Stigma receptivity occurs after anthesis and remains so for two days. Nectar is secreted in minute volume varying from 0.5-08 μ l per flower. The flowers are oriented horizontally and the stigma with inward curvature is placed beyond the height of stamens enabling the forager to strike the stigma first and then the anthers ventrally prior to probing the flower for nectar and/or pollen and effecting pollination. If the forager had the pollen on its ventral side from the previously visited flowers, then it would effect cross-pollination or else it would effect self-pollination.

The flowers were foraged by diurnal insects consisting of bees and butterflies during daytime. The bees foraged from 0700 to 1700 h with more activity during 0900-1300 h (Figure 5) while butterflies foraged from 0800 to 1300 h with more activity during 0900-1100 h (Figure 6). Bees included *Apis dorsata* (Figure 2c), *A. cerana*, *A. florea* (honey bees), *Xylocopa pubescens* (Figure 2d), *X. latipes* (large carpenter bees). Butterflies included nymphalids, *Acraea violae*, *Junonia almana* (Figure 2e), *J. lemonias* and *J. orithya* (Table 1). Bees foraged for nectar and pollen while butterflies foraged for nectar only. Bees approached the flower in upright position, struck the stigma first and then anthers with their ventral side before accessing the nectar situated at the corolla base. In this process, cross-pollination occurs if the bees had pollen from the previously foraged flowers otherwise self-pollination occurs eventually at the time of their departure from the flower. Among bees, *Apis dorsata* and *Xylocopa* bees used anther vibrations called "buzzes" to release pollen from poricidal anthers. These bees are most efficient to remove pollen by using buzzing behavior. During buzz-pollinating visit, individual bees embraced one or two poricidal anthers, holding on to the anthers using their mandibles, curled their body around the anthers, and produced few to several bursts of vibrations resulting in pollen ejection from the apical pore of the anthers. These vibrations or buzzes were quite audible and different from those vibrations that are produced during their flight. Further, the length of buzzes of the bees was comparatively more during morning hours than that of buzzes produced during afternoon hours indicating the standing crop of pollen available in poricidal anthers. *A. cerana* and *A. florea* bees never attempted to produce any anther vibrations but collected pollen that is available at the apical pore of the anthers. Butterflies landed on the lateral side of the flowers, inserted their proboscis to the base of the corolla and collected nectar. Usually, they did not contact the anthers or attempted to collect pollen. Therefore, the bees were found to be the exclusive pollinators while butterflies were nectar robbers indirectly promoting visits by nectar-seeking bees and pollinating rate.

Fruits mature within 3-4 weeks; initially green and scarlet-red when mature (Figure 2f). They are globose berries, 10-15 mm diameter and glabrous consisting of many sub-orbicular or sub-reniform compressed seeds. Fruits are indehiscent, fall to the ground by gravity and release seeds upon decomposition of pericarp covering the pulp part inside. The seeds released from the fruits subsequently germinate either at the parental site or disperse through tidal water or rain water and germinate in non-parental sites.

Table 1 List of insect foragers on *Dalbergia spinosa* and *Solanum trilobatum*

Order/Family	Insect species	<i>Dalbergia spinosa</i>		<i>Solanum trilobatum</i>	
		Pollen	Nectar	Pollen	Nectar
Hymenoptera					
Apidae	<i>Apis dorsata</i> F.			+	+
	<i>Apis cerana</i> F.	+	+	+	+
	<i>Apis florea</i> F.	+	+	+	+
	<i>Trigona iridipennis</i> Smith	+	+	-	-
	<i>Xylocopa pubescens</i> Spinola	-	-	+	+
	<i>Xylocopa latipes</i> Drury	-	-	+	+
Megachilidae	<i>Megachile</i> sp.	+	+	-	-
Lepidoptera					
Nymphalidae	<i>Acraea violae</i> F.	-	-	-	+
	<i>Junonia almana</i> L.	-	-	-	+
	<i>Junonia lemonias</i> L.	-	-	-	+
	<i>Junonia orithya</i> L.	-	-	-	+

***Typha domingensis* Pers. (Typhaceae)**

Typha domingensis is a perennial herbaceous emergent marshland or wetland weed (Figure 3a). It is widely grown in waterlogged areas in inland and coastal wetlands. The leaf and stem stand erect in a straight way; leaves are long, linear, flat on one side and convex on the other side. It also spreads prolifically by rhizomes forming large inter-connected stands or monotypes reducing wetland biodiversity. The flowering and fruiting events occur throughout the year. Inflorescences are cylindrical spikes of small monoecious flowers with male flowers produced above the female flowers on the same axis and intermixed with slender hairs.



Figure 3 a. *Typha domingensis*, b. *Saccharum spontaneum*, c-e: *Myriostachya wightiana* –c. Habit – in flowering phase, d. Inflorescence, e. Fruiting phase.

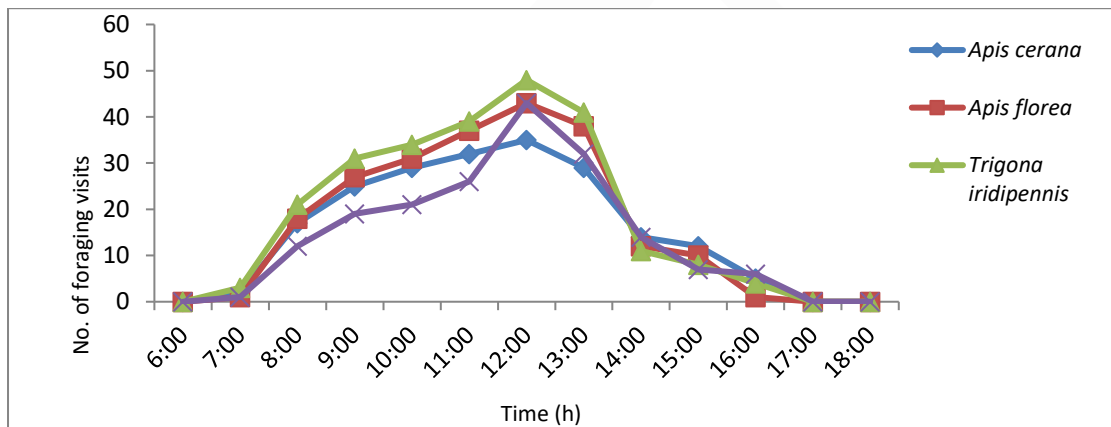


Figure 4 Hourly foraging visits of bees on *Dalbergia spinosa*

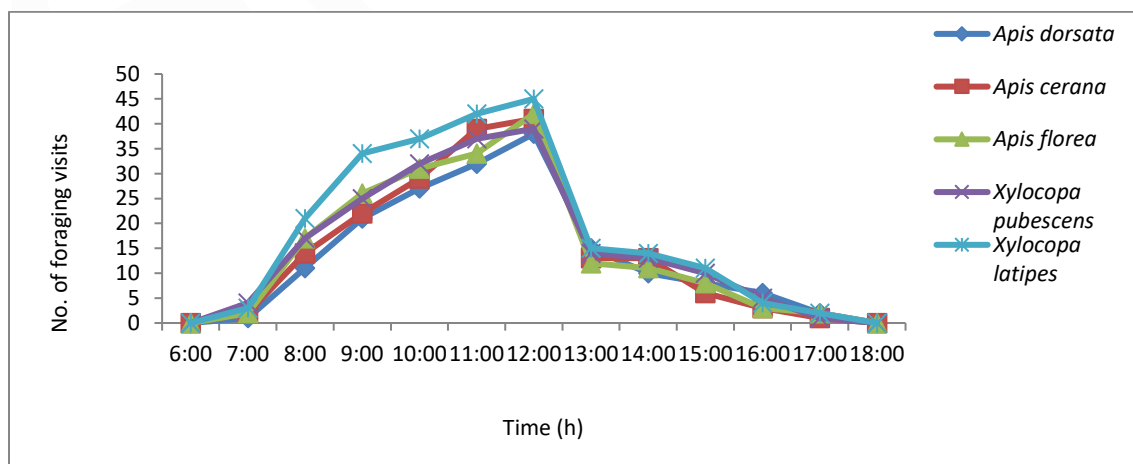


Figure 5 Hourly foraging visits of bees on *Solanum trilobatum*

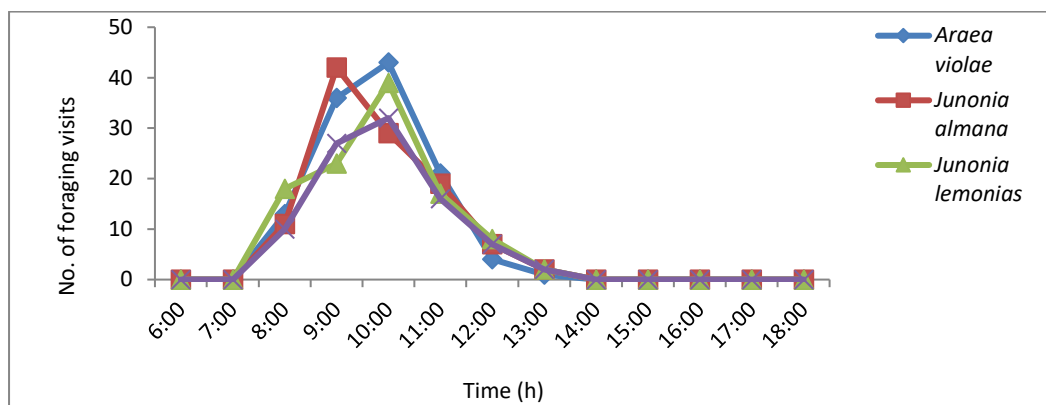


Figure 6 Hourly foraging visits of butterflies on *Solanum trilobatum*

The male and female flowers are separated by a gap of 8-10 cm naked stem. Male flowers are 5 mm long and consist a pair of yellow anthers consisting of monad pollen grains covered by hairs and wither after pollen shedding. Female flowers are 2 mm long with pistil in the center covered laterally by bractlet and hairs; the ovary long stalked, unilocular with solitary erect ovule, narrowed into a capillary style with filiform stigma. The flowers are never visited by any insects. Fruits are minute and indehiscent with membranous pericarp. Seeds are very minute and attached to fine hairs. When female spike is ripe, it disintegrates into a cottony fluff from which the seeds disperse by wind.

***Saccharum spontaneum* L. (Poaceae)**

Saccharum spontaneum is a perennial grass with spreading rhizomatous roots (Figure 3b). It reproduces vegetatively through clonal spread from underground rhizomatous roots and culm fragments. It also propagates through seeds. The dual modes of propagation are contributing to its aggressive, invasive and widespread growth in damp areas in inland and coastal habitats. In marshy and mangrove habitats, it is restricted to landward side forming a vast continuous stretch of population inhibiting the growth of other plant species in the vicinity. Vegetative growth occurs during rainy season from rhizomatous roots as well as from seeds. The rhizomatous roots exhibit dormant phase during dry season. Flowering occurs during September-November. Leaves are harsh and linear. Culms are green or grey and produce long, erect, silky white compound ovate panicles of 55-65 cm length with numerous racemes. Spikelet bearing axes are spiciform racemes with hirsute rachides. Each rachis comprises of a pair 3-4 mm long hermaphrodite spikelets of which one is sessile and the other is pedicellate. Glumes are as long as spikelets, papery and pointed with ciliate margins. Lower and upper glumes are ovate-lanceolate with ciliate margins; the former is 2-keeled in sessile spikelet while the latter is not 2-keeled in pedicellate spikelets. Lower floret is empty while upper floret is bisexual. First lemma is ovate-acute while second lemma is linear-lanceolate. Stamens are 3 and anthers are yellow. Ovary is oblong, glabrous with two long styles and each terminated with a feathery stigma consisting of simple dentate hairs.

Spikelets were never visited by any insect species even for pollen collection. The flowers produce dry powdery pollen which is easily dispersed by wind and its dispersal is further driven by swinging panicles. But, diurnal variation in temperature and humidity during flowering season was found to influence the pollen dispersal by wind. Fruits grow from pollinated flowers in 5-6 weeks time. Each fruit produces one small seed. Ripe fruits fall off as individual units comprising of pairs of spikelets together with rachis below them indicating that the unit of dispersal is a pair of spikelets, each of which has a tuft of long silky hairs at its base and make the whole unit very light in weight facilitating the dispersal unit to float in air for long distances when wind blows. Usually, several dispersal units get entangled and form a woolly or hairy mass, and dispersed massively to other areas depending on the prevailing wind speed. Seeds germinate and produce new plants in June or July depending on the occurrence of first and subsequent rains.

***Myriostachya wightiana* (Nees ex Steud.) Hook.f. (Poaceae)**

Myriostachya wightiana is a gregarious perennial grass species that grows along muddy creeks and channels in inter-tidal mangrove swamps situated on the landward side (Figure 3c). It has well developed pachymorph rhizome that produces large slow-growing horizontal determinate stems which eventually produce vertical flowering culms. Reproduction takes place by rhizome and via seed. Rhizomes continually give off new culms which get separated subsequently for growth as individual plants. Sexual reproduction takes place through pollination and fertilization of flowers. Flowering occurs mostly during late rainy season during August-November but sporadic flowering occurs throughout the year if muddy soils are saturated with creek water. Leaves are mostly basal,

linear, glabrous and acuminate. Culms are tall and densely tufted. Inflorescence is composed of numerous 3-10 cm long racemes borne along a 30-65 cm long central axis (Figure 3d). Racemes bear pedicellate spikelets comprising varying number of bisexual florets. Glumes are shorter than spikelets, lower glume lanceolate, membranous and 1-keeled while upper glume is awned with acuminate apex. Lemma are ovate, membranous and keeled. Palea oblong with ciliolate keels. Lodicules are 2, fleshy and truncate. Stamens are 3, linear and anthers versatile. Ovary is globose, glabrous, monocarpellate with one ovule; styles are 2 and each style has a feathery stigma. Flowers were never visited by any insect species. Pollen is dry and powdery, and dispersed by wind due to direct exposure of anthers to sunlight.

Fruits mature in 3-5 weeks time (Figure 3e). Fruit is a caryopsis, indehiscent and 1-seeded in which the ovary wall is united with the seed coat. Ripe fruits fall off as individual units comprising of spikelets indicating that the unit of dispersal is spikelet, The fruits have a tuft of hairs making the dispersal unit very light in weight in order to enable itself to float in air for long distances when wind blows. Usually, several spikelets get entangled and form hairy mass, and dispersed massively to other areas depending on the prevailing wind speed. Seeds germinate upon decomposition of fruit pericarp and produce new plants in June or July depending on the occurrence of first and successive rains.

4. DISCUSSION

All five plant species, *Dalbergia spinosa*, *Solanum trilobatum*, *Typha domingensis*, *Saccharum spontaneum* and *Myriostachya wightiana* are mangrove associate species. They grow in marshy swamps and mangrove habitats along the backwater creeks adjoining the landside. Of these, *D. spinosa* and *S. trilobatum* are shrubs but the first one grows to a small tree in nutrient-rich environment; they also grow in damp places in inland habitats. *T. domingensis* is a forb while *S. spontaneum* and *M. wightiana* are grasses; these species also grow near freshwater ponds and roadside ditches. The occurrence of all these species in both freshwater and saline habitats indicates that they have adaptations to live in non-saline and saline muddy soils. However, their occurrence in coastal wetland areas is restricted to creek banks adjoining the land side and hence qualifies for the designation of "oligohaline" species. All these species flower and fruit seasonally but they continue these events sparsely throughout the year in damp soils saturated with freshwater or tidal water.

Vasuadeva and Sareen (2009) reported that *Dalbergia* species are typically pollinated by honeybees, beetles and butterflies. Frankie et al. (2002) reported that pollen is dispersed by bees in *D. glomerata*, *D. stevensonii* and *D. retusa*. In the present study, it is found that *D. spinosa* produces typical papilionaceous flowers which are small, bisexual and zygomorphic. The flowers are diurnal in function because they are open in the morning and close by the evening of the same day. They exhibit explosive pollination mechanism adapted for tripping by appropriate forage collecting insects. This study noted that honey bees and leaf cutter bees activate the pollination mechanism by tripping keel petals in which the stamens and stigma are under tension and gather both nectar and pollen during which they effect either cross- or self-pollination. Therefore, *D. spinosa* is typically melittophilous.

Marin and Flores (2003) reported that seed dispersal occurs by wind and water in *Dalbergia retusa* and *D. stevensonii*. In this study, it is found that *D. spinosa* produces indehiscent 1-seeded light weight pods adapted for wind dispersal from the parental plants and for water dispersal on the soil floor. Therefore, *D. spinosa* is both anemochorus and hydrochorus.

Rasolomampianina et al. (2005) and Sprent (2009) reported that *Dalbergia* species form root nodules in symbiosis with nitrogen-fixing soil bacteria and with this ability, they play an important role in enhancing soil fertility and biodiversity sustainability. *D. spinosa* with nitrogen-fixing ability is very important in promoting soil fertility in muddy and marshy areas in the estuarine zone and in consequence, other mangrove associate or true mangrove plant species growing in the area will be benefitted.

Muthukumar et al. (2012) noted that *Solanum trilobatum* is a mangrove associate herb. Panda et al. (2013) mentioned that *S. trilobatum* is a back mangrove and flowers during May-March. In this study, it is found that *S. trilobatum* is a perennial mangrove associate with shrubby habit growing as a back mangrove due to its restriction to muddy and marshy soils in oligohaline zone of the mangrove habitats. It flowers prolifically during July-October and sporadically outside this period if the soil environment is sufficiently wet.

Buchmann (1983) reported that most buzz-pollinated plants keep pollen locked inside tubular, non-dehiscent poricidal anthers. Corbet and Huang (2014) noted that buzz-pollinated plants keep anthers inside closed corolla tubes with apical openings to restrict direct access to pollen. De Luca and Vallejo-Marin (2013) reported that pollen grains from poricidal anthers of buzz-pollinated flowers are most efficiently removed by bees by causing floral vibrations. These authors and Cardinal et al. (2018) mentioned that little is known why some bee species such as carpenter bees, bumblebees, sweat bees buzz-pollinate while others appear incapable of floral vibrations to buzz-pollinate the flowers. In this study, it is found that *S. trilobatum* is a diurnal bloomer and produces nectariferous flowers with poricidal anthers. The flowers remain attached to the flowers for more than two days enhancing attraction to pollinator insects. Further, the gradual release of pollen from poricidal anthers through floral vibrations caused by bees, the

position of stigma beyond the height of stamens and the 2-days long period of stigma receptivity appear to indicate that the plant is predominantly out-crossing. All bees also first strike the stigma prior to proceeding to collect nectar or pollen; in this act, cross-pollination is certain if they had pollen from the previously visited flowers. Carpenter bees and the large-bodied honey bee, *Apis dorsata* caused floral vibrations by holding the anthers to enable the dehiscent anthers to eject pollen from their apical pore. The pollen thus ejected is gathered by them sternotribically. Other honey bees recorded on the flowers appear to be incapable of buzz-pollinating which could be probably due to their small body size. Butterflies act as nectar robbers only because they bypass the sex organs while probing the flower for nectar. Therefore, *S. trilobatum* is buzz-pollinated by carpenter bees, large-bodied honey bee and conventionally pollinated by other honey bees. Nevertheless, this plant species is characteristically melittophilous.

S. trilobatum produces indehiscent pulpy fruits which upon detachment disseminate to the ground by gravity. The fallen fruits release seeds upon decomposition of the pericarp. The seeds thus released germinate either at parental site or at non-parental sites. In the latter case, the seed dispersal occurs through rain or tidal water which characterizes the function of hydrochory. Therefore, *S. trilobatum* is barochorous and hydrochorous. Kumar et al. (2011) and Swathy et al. (2010) documented that *S. trilobatum* is used to cure respiratory problems, bronchial asthma, snake poison, increase male fertility and tuberculosis. Since the plant has many medicinal uses, it can be utilized in traditional medicine and its periodical harvest from its growing areas is an effective way of clearing the area to enable other native plant species to come up and populate the area in order to contain biodiversity.

Van der Valk and Davis (1976) reported that *Typha* species are usually the first wetland plants to colonize areas of newly exposed wet mud with their abundant anemochorous seeds. Further, these species have the ability to spread by rhizomes and form large interconnected stands. In this study, it is found that *T. domingensis* grows prolifically both in inland and coastal wetland habitats. It is widespread in the study area due to its dual modes of reproduction, vegetative (by rhizomes) and sexual (by seed). It is a year-long bloomer if soil is sufficiently wet. McNaughton (1966) mentioned that some populations of *T. domingensis* display anthesis for more than a month. In this study, it is found that *T. domingensis* produces cylindrical spikes which show anthesis for more than two months depending on the number of spikelets produced by individual spikes. Smith (1967) mentioned that *T. domingensis* is protogynous, self-compatible and apomixis is non-functional. The present study found that *T. domingensis* is monoecious with female and male spikelets produced on the same axis but both sexes are separated by a naked stem or culm. The male buds open first and after pollen shedding from most of the flowers over a period of 2-3 weeks, the female buds open and continue until the last buds complete anthesis. Male spikelets fall off as soon as they shed pollen while female flowers remain in place and produce fruits, one seed from each fruit. The monoecious sexual system, in principle, is an indication that plants that possess this sexual system are self-compatible but it promotes cross-pollination by reducing self-pollination through geitonogamy. However, this sexual system is characteristically vector-dependent, in *T. domingensis*, it is wind that acts as vector to effect pollination since insects do not visit the spikes as there is no nectar in both flower sexes and anthers in male flowers are minute, invisible and not recognizable by them. Further, the feathery and hairy stigmas swinging openly are specialized to capture the wind-driven powdery pollen passing through them. Therefore, *T. domingensis* is exclusively anemophilous. Howard-Williams (1975) reported that *T. domingensis* produces more than 6,00,000 fruits or 6-17 million seeds per m². The present study finds that *T. domingensis* could produce more than the number given by him and it is also difficult to count them manually. Fruits are 1-seeded, indehiscent and disperse by wind when female spike disintegrates into a cottony fluff. Therefore, *T. domingensis* is anemochorous.

Mukherjee (1957) reported that *Saccharum spontaneum* is a polymorphic species. Daniels and Roach (1987) and Tai and Miller (2001) noted that *S. spontaneum* is highly adaptable polyploid and hence grows well in a wide range of habitats across southern Asia and east Africa to the Mediterranean. Panje (1970) and Yadav et al. (2007) reported that *S. spontaneum* with its potential to propagate via seeds and aggressive rhizomatous spread has become a widespread weed. The present study found that *S. spontaneum* with the ability to reproduce vegetatively by rhizomes and sexually by seed is extensively invasive and has the ability to colonize damp places or water-logged areas in inland and coastal habitats. Panje and Srinivisan (1959) reported that *S. pontaneum* shows vegetative growth during wet monsoon season and becomes dormant during dry season. Flowering in this species occurs at the end of rainy season and pollen and seed dispersal events are influenced by diurnal variations in humidity and temperature. In this study, it is found that flowering occurs during late part of southwest monsoon season during northeast part of rainy season and its rhizomes and seeds are dormant during dry season. Inflorescences produce huge numbers of bisexual flowers with anthers producing dry powdery pollen easily liberated into the air and the swinging feathery and hairy stigmas. The flowers with these traits are well suited for pollination by wind; minute flowers, non-production of nectar and non-visitation of flowers by insects further substantiate that this plant species is adapted for wind-pollination. Therefore, *S. spontaneum* is exclusively anemophilous. In *S. spontaneum*, fruits are 1-seeded and fall off as individual units comprising of pairs of spikelets along with rachis attached below them. Each spikelet has a tuft of long silky hairs at the base making the unit very light in weight. These characters of fruits covered

hairy structures enable them to fly in air when wind blows. However, several units of pairs of spikelets detach as clumps of woolly or hairy mass for dispersal by wind. Therefore, *S. spontaneum* is anemochorous.

Sahu et al. (2015) reported that *Myriostachya wightiana* is an important salt marsh in mangrove habitats. Rashid and Ahmed (2011) reported that it has a wide range of distribution throughout saline swampy mangrove areas due to its anatomical adaptive features such as thick epidermis in stem, leaf and root, development of sclerenchyma tissues in vascular system, salt secretory glands in the leaf, prominent metaxylem and large phloem area in stem and leaf, thick cortex and lignification of exodermis in the root. In this study, it is found that *M. wightiana* is a gregarious mangrove associate growing along muddy creeks and channels in inter-tidal mangrove swamps. Its gregarious growth and invasiveness is related to its ability to grow vegetatively by pachymorph rhizome and sexually by seed. Flowering is seasonal occurring during rainy season; however sporadic flowering occurs outside this season. The racemose inflorescences produce minute bisexual flowers with anthers producing powdery and dry pollen, feathery and hairy stigma, and lacking nectar. These floral traits indicate anemophilous syndrome. Since the flowers are never visited by any insect species during its flowering season, wind is agent to effect pollination in this species. Therefore, *M. wightiana* is anemophilous. In *M. wightiana*, fruit is an indehiscent 1-seeded caryopsis with a tuft of hairs enabling it to fly in air. Dispersal unit is fruit-bearing spikelets with hairy mass which detach as clumps and disperse by wind. Therefore, *M. wightiana* is anemochorous.

5. CONCLUSIONS

All five plant species are oligohaline mangrove associate species but they also grow in inland freshwater habitats. *T. domingensis* is monoecious with male and female flowers occurring on the same inflorescence axis while all other species are hermaphroditic. *D. spinosa* displays explosive pollination mechanism while *S. trilobatum* displays buzz-pollination mechanism; both species are melittophilous while the other three species are anemophilous. *D. spinosa* is anemochorous and hydrochorous, *S. trilobatum* barochorous and hydrochorous, and all other species are hydrochorous. All these species are ecologically important to check soil erosion effectively, add fertility to soil and useful in traditional medicine. Further, *T. domingensis*, *S. spontaneum* and *M. wightiana* are useful for making thatched houses and handicraft products. Therefore, these species can be exploited for human use if they become nuisance and create an ecological havoc in areas where they are invasive.

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Author's contributions

All authors contributed equally.

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