REPRODUCTIVE ECOLOGY OF *BRUGUIERA CYLINDRICA* (L.) BL. (RHIZOPHORACEAE), A TRUE VIVIPAROUS MANGROVE TREE SPECIES IN CORINGA MANGROVE FOREST, ANDHRA PRADESH (INDIA)

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ABSTRACT

Bruguiera cylindrica (L.) Bl. bloom during September-March. It is hermaphroditic, protandrous, self-compatible and facultative xenogamous. The flowers possess an explosive pollination mechanism and are pollinated by bees and wasps. The pollination mechanism is characterized by special petal-stamen configuration in which each petal encloses two stamens and becomes tensed after anthesis. Each petal behaves independently and the explosion of all petals of a flower requires one or two visits. Individual flowers produce only one seed which produces seedlings on the maternal plant. The seedlings use self-planting strategy at low tide and stranding strategy at high tide. Both strategies are useful for regeneration in maternal environment and in areas away from material environment.

ZUSAMMENFASSUNG: Fortpflanzungsökologie von *Bruguiera cylindrica* (L.) Bl. (Rhizophoraceae), eine echte vivipare Mangrovenbaumart im Coringa Mangrovenwald von Andhra Pradesh (Indien).

Bruguiera cylindrica (L.) Bl. blüht von September bis März. Sie ist eine hermaphrodite, protandrische, selbst-kompatible und fakultativ xenogame Art. Die Blüten besitzen einen explosiven Bestäubungsmechanismus und werden von Bienen und Wespen bestäubt. Der Bestäubungsmechanismus ist durch eine spezielle Blütenblatt-Staubgefäße-Konfiguration gekennzeichnet, bei der jedes Blütenblatt zwei Staubblätter umschließt, die sich nach dem Verblühen straffen. Jedes Blütenblatt verhält sich unabhängig eines vom anderen und die Explosion aller Blütenblätter einer Blüte benötigt einen oder zwei Bestäuberbesuche. Einzelne Blüten erzeugen nur einen Samen, der einen Keimling an der Mutterpflanze entwickelt. Die Keimlimge verwenden eine Selbstpflanzungsstrategie während der Ebbe und eine Grundberührungs- bzw. Strandungsstrategie während der Flut. Beide Strategien sind für die Regenerierung im Umfeld der Mutterpflanze von Nutzen sowie auch in entfernter gelegenen Gebieten.

REZUMAT: Ecologia reproducerii speciei *Bruguiera cylindrica* (L.) Bl. (Rhizophoraceae), o adevărată specie vivipară lemnoasă în pădurea de mangrove de la Coringa, Andhra Pradesh (India).

Bruguiera cylindrica (L.) Bl. înflorește din septembrie până în martie. Este hermafrodită, protoandrică, auto-compatibilă și facultativ xenogamă. Florile posedă un mecanism explosiv de polenizare, fiind polenizate de albine și viespi. Mecanismul de polenizare are o configurație de petală-stamine, cu două stamine la fiecare petală, care se netezesc după anteză. Fiecare petală se comportă independent, iar explozia tuturor petalelor unei flori necesită una sau două vizite ale speciilor polenizatoare. Florile individuale produc o sământă, care dezvoltă un germen pe planta maternă. Germenii florilor folosesc o strategie de autoplantare în timpul refluxului și o strategie de aruncare la țărm în timpul fluxului. Ambele strategii sunt utile pentru regenerarea în apropierea plantei mamă dar și pentru cea îndepărtată de aceasta.

INTRODUCTION

Mangrove frests are among one of the world's most productive tropical ecosystems (Roy and Krishnan, 2005). They are important in protecting coasts from erosion by fierce tides, in promoting the diversity of marine organisms and fisheries by contributing a quantity of food and providing favourable habitats for animals (Bandaranayake, 1998; Zheng et al., 1999; Kathiresan, 2003a, b). They are sources of timber, fuel wood, poles, thatching material, grass, honey, wax and industrial raw material (Zhengyun et al., 2003) but they are under immense threat worldwide due to their multiple economic uses and alterations of freshwater inflows by various upstream activities in catchment areas (Blasco et al., 2001). Therefore, there is an immediate need for their effective conservation and management in order to use them sustainably (Alang et al., 2010; Aziz and Hashim, 2011; Sabai and Sisitka, 2013).

Little is known about pollination and seedling ecology despite the fact that this information is important to understand regeneration and distribution of mangrove flora. Few scientists reported on mangrove plants with reference to their interaction with pollinators for pollination and the level of reproductive effort needed by them to produce a single propagule and whether there is any resource or pollinator limitation in propagule production (Coupland et al., 2006). Such a state of information warrants for detailed studies on all aspects of reproductive ecology of mangrove plant species in all areas of their distribution in the world. In India, *Bruguiera* genus is represented by four species, *B. gymnorrhiza*, *B. sexangula*, *B. parviflora* and *B. cylindrica*; the first two species produce large and solitary flowers while the last two species produce small and many-flowered clustered inflorescenes (Tomlinson, 1986). In these species, the stamens remain enclosed in pairs within the petals under tension after flower-opening, and the pollen release occurs explosively when the flower is triggered. Birds trigger the process in the large-flowered species, while butterflies trigger the process in small-flowered species (Juncosa and Tomlinson, 1987; Chiou-Rong et al., 2005). *B. gymnorrhiza* has mixed mating system with out-crossing as a main mating system (Ge et al., 2003). Reproductive ecology information is totally lacking for all other *Bruguiera* species. Therefore, the present study provides information on the reproductive ecology of *Bruguiera cylindrica* (L.) Bl., occurring in Coringa mangrove forest in the State of Andhra Pradesh, India.

MATERIALS AND METHODS

Bruguiera cylindrica distributed in the Coringa Mangrove (16°30'-17°00'N and 82°10'-80°23'E) (Fig. 2) in the State of Andhra Pradesh, India, was used for the study during February 2015 – April 2017. This species is represented by a few individuals with scattered occurrence in this forest. The present state of this species is attributed to its use as fuel wood and as source material for the construction of traditional homes and furniture. The flowering season, floral biology, pollen production, nectar analysis, breeding system, natural fruit set, stigma receptivity, pollination mechanism, pollinators and seedling ecology were investigated following the protocols described in Dafni et al. (2005). Foragers captured from flowers were washed in ethanol for pollen separation and they were then stained with aniline-blue on a glass slide for observation under microscope in order to count pollen grains present. This procedure was repeated for each capture forager specimen. Then, the mean number of pollen grains present on the body of each species was calculated separately to record the pollen carrying rate.

RESULTS

It is a medium evergreen tree with diffused spreading branches, growing to a height of more than 12 m (Fig. 1a). The flowering occurs during September-March. The inflorescence is a simple pedunculate dichasium cyme with pedicellate erect flowers; each cyme is three-flowered and borne in leaf axils (Figs. 1b, c).

The mature buds open during 07.00-09.00 h. The sepals diverge gradually presenting the closed, erect petals in the cocked position (Figs. 1d-f). The petals enclose the stamens in tensed state due to the pressing of the latter against the interlocked margins of the petals (Fig. 1g). The petals are retained in an erect position by the adherent ventral margins. The anther dehiscence occurs in mature buds by longitudinal slits. A delicate touch to the petal margins would result in release of the anthers which simultaneously eject pollen to the centre of the flower. In case of touch by forager to the petal margins, the pollen would be ejected and deposited on the head and body. In a flower, petals unzip independently and non-violently. The unzipped petals stay back against the calyx lobes during which the stamens are empty, twisted and also disorganized. Petals and stamens last three days in unzipped flowers. Unzipped petals stay in tensed state for six days after which they fall off. Stigmatic lobes are receptive on 2nd and 3rd day (Fig. 1h). Individual flowers produce a mean number of 20,635 pollen grains and pollen-ovule ratio is 5,518: 1. The pollen grains are light yellow, powdery, tricolporate and 16.6 µm long. Nectar is secreted in the calyx cup which is surrounded by hairs; it is 1.43 ± 0.31 µl per flower. The nectar sugar concentration is 15.2 ± 1.57% with glucose, fructose, sucrose and maltose but the first sugar is dominant. The flowers are self-compatible and self-pollinating. Fruit set occurs in unmanipulated and manipulated autogamy, geitonogamy and xenogamy but it is highest in the last mode. Further, fruit set stands at 64% in open-pollinations which are affected by foragers (Tab. 1).

The flowers were foraged during day time from 07.00-17.00 h by one bee and two wasp species; the former for pollen and nectar while the latter for only nectar (Fig. 2). The bee made 38% and wasps 62% of total foraging visits (Fig. 3). While probing the flowers for forage, they invariably tripped the tensed petals due to which the petals exploded and ejected pollen. The petal tip and its apical appendages are insensitive but vigorous probing into the calyx cup by foragers caused petal tripping. One or two visits to individual flowers caused all petals to unzip and release pollen. The foraging visits resulted ended in pollination. The foragers visited the flowers of different conspecific plants frequently seeking more forage due to the occurrence of a few rewarding flowers daily on individual trees; this foraging activity made them disperse pollen across individual trees which are spatially isolated; such pollen dispersal pattern contributed to both self and cross pollination. Bees and wasps carried pollen on their bodies and the mean number of pollen grains ranged from 262 to 448.2 (Tab. 2).

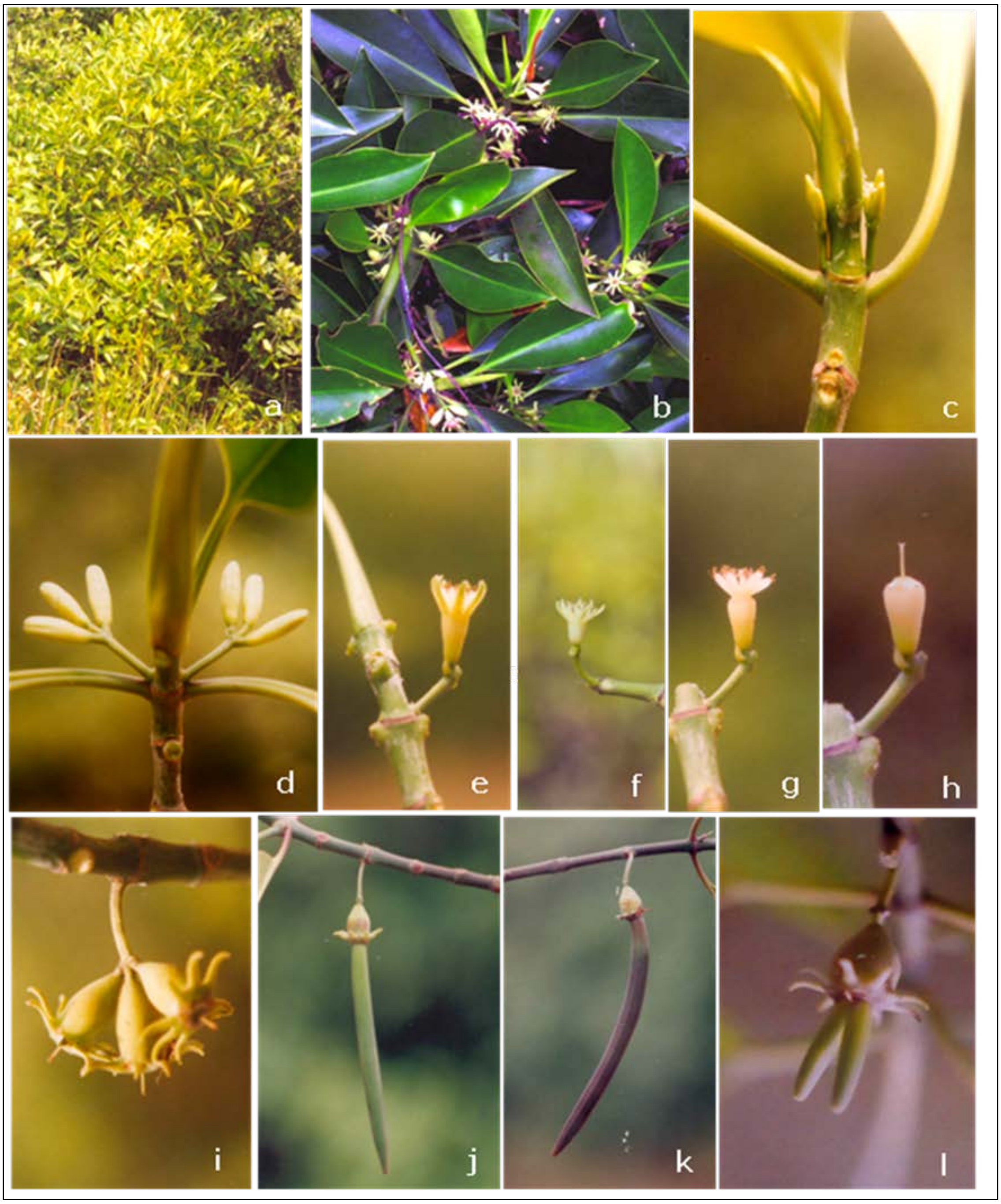

Figure 1: *Bruguiera cylindrica*: a. Habit; b. Tree with flowering; c. Cymes emerging from the axils of leaves; d. Mature buds; e. Anthesing bud; f. Fully open flower; g. Stamens enclosed in petals; h. Style with bifid stigma; i. Mature fruits; j. Green hypocotyl; k. Purple hypocotyl; l. Fruit with two hypocotyls.

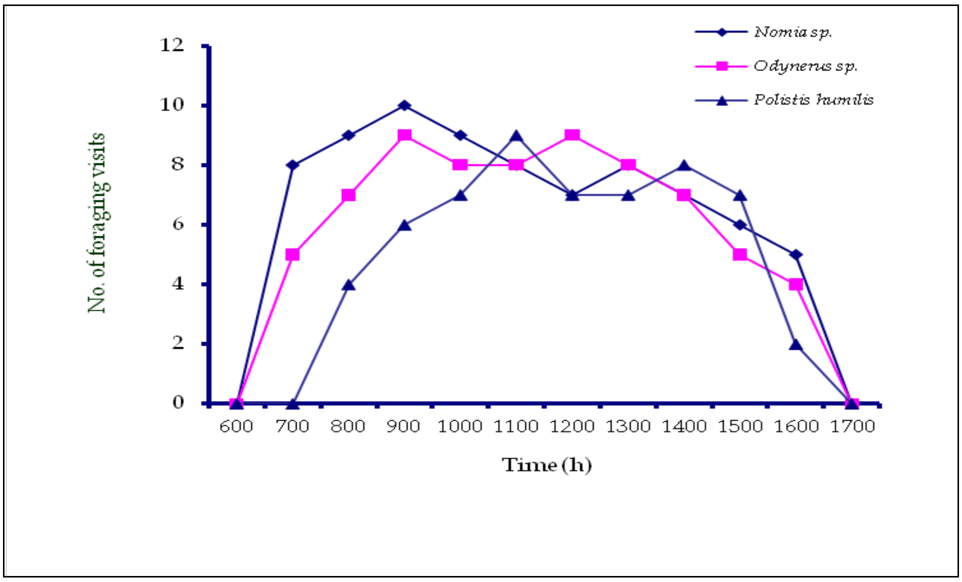

Figure 2: Hourly foraging activity of insects on *Bruguiera cylindrica*.

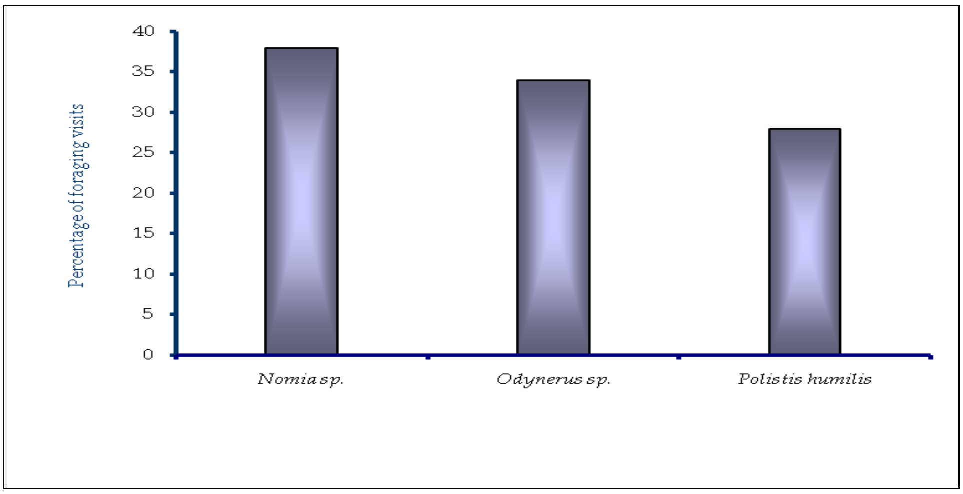

Figure 3: Percentage of foraging visits of insects on *Bruguiera cylindrica*.

Fruits mature in about three weeks (Fig. 1i). Each fruit produces only one seed although each flower produces four ovules. The production of two seeds by a fruit is a rare event (Fig. 1l). Individual seeds produce cylindrical elongate but slightly curved, green to purple, pendulous seedlings with blunt apex in four weeks (Figs. 1j, k). The seedlings anchor in the mud at low tide when the forest floor is exposed or float in and disperse by tidal currents at high tide. The chronological events of reproduction are listed in table 3.

Table 1: Results of breeding experiments on *Bruguiera cylindrica*.

Breeding system	No. of flowers pollinated	No. of flowers set fruit	Fruit set (%)
Autogamy (bagged)	30	12	40
Autogamy (hand-pollinated and bagged)	25	14	56
Geitonogamy	30	19	63.3
Xenogamy	30	24	80
Open pollinations	73	47	64.4

Table 2: Pollen pick up efficiency of foraging bees on *Bruguiera cylindrica*.

Bee species	Sample size	Range	Mean ± S. D.
Nomia sp.	10	210-642	448.2 ± 93.8
Odynerus sp.	10	126-520	342 ± 78.09
Polistis humilis	10	116-426	262 ± 60.7

Table 3: Chronology of floral and fruiting aspects in *Bruguiera cylindrica*.

Floral event	*B. cylindrica*
Anthesis	07.00-09.00 h
Anther dehiscence	Mature bud
Sepals	Not reflexed throughout flower life and persistent even after propagule detachment
Petals	Up to three days
Stamens	Up to three days
Stigma receptivity	2nd-3rd day
Pollen output/flower	20,635
Pollen-ovule ratio	5,158:1
Nectar volume/flower (µl)	1.43 ± 0.31
Nectar sugar concentration (%)	15.2 ± 1.57
Nectar sugars	Glucose, fructose, sucrose and maltose
Pollination mechanism	Explosive mechanism
Pollinators	Bee and wasps
Breeding system	Self and cross
Fruit set in open pollinations (%)	64.4
Fruit maturation time (days)	18-20
Hypocotyl length (mm)	136 ± 16
Hypocotyl orientation	Hanging
Hypocotyl growth duration (days)	30-35
Planting strategy	Self-planting and stranding

DISCUSSION

Bruguiera cylindrica blooms uniformly during September-March. Pollinator activity is not intense and also inconsistent on the flowers. The long period of flowering enables the plant to maximize fruit set rate. The flowers project outwards from the crown of leaves. They display different orientations, horizontal, downward and slightly erect – these orientations enable the foragers to collect forage with ease. The morning anthesis with flowers providing forage day long coincides well with day-active foragers. The described floral characteristics suggest that the plant has specialized explosive pollination mechanism adapted for insects, bees and wasps in the study area. This pollination mechanism is the characteristic of *Bruguiera* genus (Tomlinson et al., 1979). *B. cylindrica* with small flowers is reported to be pollinated by butterflies by Tomlinson et al. (1979) and by small insects including butterflies by Tomlinson (1986). In the study site, *B. cylindrica* is pollinated by insects consisting of bee and wasp species only. They use the nectar with low sugar concentration with hexose-dominant sugars produced by *B. cylindrica* but this nectar is produced in small quantity at flower level forcing these insects to make multiple visits across spatially isolated plants and the process cross-pollination is promoted. The nectar quantity and quality characters displayed by this plant agree partially with the generalization made by Baker and Baker (1983) who stated that bee-flowers characteristically produce a small quantity of nectar with high sugar concentration and the flowers adapted for pollination by short-tongued bees produce hexose-rich nectar while wasp-pollinated flowers produce sucrose-rich nectar. Tomlinson (1986) reported that bees and wasps nest in mangroves, and some of their populations are completely dependent on mangrove plants for their survival. Similarly, Ghosh et al. (2008) also mentioned that some wasps and flies use mangrove plants for nesting. Therefore, bees and wasps are reliable as pollinators since they nest in mangroves and use the same plants as food sources.

B. cylindrica is facultatively xenogamous as it produces fruit set in both self- and cross-pollination modes but all modes of pollination are vector-dependent. The ability to fruit through selfing enables this plant to set fruit even isolated trees if pollinators are present in the habitat. The flowers are four-ovuled but each fruit produces only one seed and very rarely two seeds. This state of seed set appears to be related either to maternal resource constraint or maternal regulation of seed set.

In *B. cylindrica*, the seed produces seedling on the mother plant. The seedling pierces through fruit pericarp and remains naked until it is separated from the fruit. This mode of seed germination is a characteristic of “true viviparous” species (Tomlinson, 1986) and allows seedlings to develop tolerance to salinity prior to detaching from the fruit or plant (Smith and Snedaker, 1995). It allows the seedlings to produce photosynthate and store nutrients before their detachment, acquire floating ability for dispersal and quick rooting in the mudd (Kathiresan, 2003). Therefore, a suite of characteristics associated with vivipary ensures the plant to overcome the tidal environment for seedling establishment and subsequent growth.

Van Speybroeck (1992) reported that the *Bruguiera* seedlings establish either by self-planting or by stranding strategy depending on the height of the tide, low or high. In this study, it is found that *B. cylindrica* seedlings disperse both self-planting and stranding strategies according to the tide level. The self-planting strategy facilitates establishment in undisturbed mangrove forest while the stranding strategy facilitates establishment in exploited and open mangrove forest. These two plant strategies are important for this plant for regeneration in the vicinity of parental environment and in areas far away from parental environment.

CONCLUSIONS

Bruguiera cylindrica is an evergreen true viviparous tree species. It is hermaphroditic, self-compatible, self-pollinating and facultative xenogamous. The flowers have explosive pollination mechanism and functional only when it is unzipped by bees and wasps or else they fall off without fruit set. Seedlings are produced while fruit is still attached to the parent tree and detach when time is ripe for them. The fallen seedlings settle at the parental environment using self-planting strategy or outside the parental environment using stranding strategy.

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