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Reproductive ecology of mangrove trees *Ceriops decandra* (Griff.) Ding Hou and *Ceriops tagal* (Perr.) C.B. Robinson (Rhizophoraceae)

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Ceriops decandra and *C. tagal* are evergreen trees in the inner mangrove forests in Andhra Pradesh, India. *Ceriops decandra* is primarily a landward species whereas *C. tagal* is a seaward and highly salt tolerant species. *Ceriops decandra* produces flowers and fruits continuously throughout the year while *C. tagal* produces flowers and fruits during winter only. Both species have a mixed mating system with cross-pollination as the principal system and self-pollination, which is primarily vector-dependent. *Ceriops decandra* flowers have a simple pollination mechanism that is adapted for pollination by daytime foragers, *Nomia* bees and *Odynerus* wasps. In contrast, *C. tagal* flowers have an elaborate and explosive pollination mechanism. Flies and honey bees trip the flowers and contribute to explosive pollen release and subsequent self- and cross-pollination. Wind is also effective in tripping the pollination mechanism but it largely contributes to self-pollination. Bud abortion occurs only in *C. decandra*. Flower and fruit abortion occurs in both the species of *Ceriops*. Abortion at different stages of the reproductive unit has been considered to be a strategy by the plants to adjust the available maternal resources to the growing fruits and propagules. The paper provides the basis for further study for the conservation and management of *Ceriops* species in the study areas.

Keywords: *Ceriops decandra*, *Ceriops tagal*, pollination, mating, vivipary, mangrove.

Introduction

Limited studies have been devoted to pollination biology and mating systems, and for mangroves the records of flower visitors and potential pollinators are mostly fragmental (TOMLINSON 1986; SOLOMON RAJU 1990 a, b; SUBBA REDDI et al. 1995). The knowledge of these aspects is a prerequisite to provide guidance for the conservation, planning and management of mangroves in view of their overexploitation throughout their distribution range.

The genus *Ceriops* consists of two species, *C. decandra* and *C. tagal*; the former more often grows within the tidal zone mixed with other Rhizophoraceae species while *C. tagal* occurs in harder and higher muddy soil of the polyhaline zone, and forms pure stands on

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better drained soils and shows stunted growth in exposed and highly saline sites (AKSORNKOAE et al. 1992, SELVAM and KARUNAGARAN 2004, TOMLINSON 1986). These two species are viviparous which means that the seed produces propagules while on the mother plant and then drops off for dispersal.

In the state of Andhra Pradesh, *C. decandra* is a common constituent of Krishna and Coringa mangrove forests while *C. tagal* is restricted to Krishna mangroves only. In this paper we report on the ecology of sexual reproduction and seed dispersal in *C. decandra* and *C. tagal* in Krishna and Godavari Mangrove forests respectively.

Materials and methods

Field studies were conducted with twenty five trees of *Ceriops decandra* (at Coringa) and with fifteen trees of *C. tagal* (at Krishna) from flowering through seedling fall, during 2004–2006. Floral structural and functional details as well as nectar characteristics were examined according to protocols (DAFNI et al. 2005, ROUBIK 1995, BAKER and BAKER 1973). Flower visitors were observed for their role in effecting pollination. Hourly foraging visits during the entire foraging period were counted on a selected number of branches with flowering inflorescences. The percentage of foraging visits for each forager species was calculated based on the daily total visits from five censuses performed on different days. Ten individuals of each forager species were captured, washed in aniline blue on a glass slide and the number of pollen grains counted under a microscope to determine their role in pollen transfer. In case of *C. tagal*, the role of wind in petal explosion and subsequent pollination was also observed during day time. For this, five easily accessible inflorescences with newly open flowers exposed to direct sunlight towards the creek in the windward direction were tagged and bagged carefully on the evening of the previous day; bags were removed carefully on the morning of the next day and the tagged inflorescences were observed at close quarters until late evening to note whether petal explosion occurred.

In case of *C. decandra*, twenty five mature buds, five each from five trees were used for each mode of pollination – autogamy, geitonogamy and xenogamy (DAFNI et al. 2005). Twenty inflorescences each (tagged) were used to record bud, flower and fruit abortion rates and natural fruit set. Four inflorescences each from five trees were selected for this purpose. Twenty inflorescences of *C. tagal*, five each from four trees, were used for fruit/seedling production to judge whether breeding system is vector-dependent. Ten tagged inflorescences, five each from two trees were used to note flower abortion rate. Sixty four open and tagged inflorescences from ten trees were used to record natural fruit set and fruit abortion at the site. In both species, the colour was used as an indicator of healthy and unhealthy propagules with the former's colour changing from green to reddish brown or dark and from green to yellow in the latter type. The percentage of such propagules is noted as fruit abortion rate.

Fruit seedling development and characteristics were also investigated in detail by following fruited flowers until propagules dropped. Visual observations on the dispersal and establishment of propagules at the study sites were made to understand the planting strategy. Some hypocotyls about to fall were tagged on the mother plants of both species in a particular area. Field studies were made in different areas for their occurrence and subsequent settlement.

Results

Both the species of *Ceriops* are evergreen shrubby tree species. Flowering and fruiting occurs throughout the year in *C. decandra* but *C. tagal* flowers seasonally, during November-February. The associate plants of *C. tagal* such as *Aegiceras corniculatum*, *Lumnitzera racemosa* and *Bruguiera gymnorhiza* flower simultaneously. The last species is a year-long bloomer.

In both the species, the flowers are born in condensed short-stalked cymes. An inflorescence produces on average 15.73 flowers (range 5–31) in *C. decandra* and on average 11 flowers (range 7–17) in *C. tagal*. The flowers are sessile and odourless in *C. decandra* but are short-stalked and fragrant in *C. tagal*. In both the species, they are small, white, cup-shaped, bisexual and zygomorphic. The sepals are five, small, light green, valvate enclosing the inner parts until anthesis and not reflexed after anthesis. The petals are five, free, two-lobed, and alternating with the sepals but they are light green in *C. decandra* and white and pubescent in *C. tagal*. In *C. decandra*, the petals are inter-locked marginally by basal short hairs and this circumstance produces a short corolla tube crowned by the series of clavate filamentous appendages. In *C. tagal*, the lower margins of adjacent petals are held together by patches of tightly intertwining, helically coiled hairs. Each petal has three distinct clavate appendages on its distal margins. In both the species, the stamens are 10, five of them antisepalous, five others antipetalous and all ten inserted on the rim of the calyx cup. In *C. decandra*, each stamen extends beyond the height of the stigma; anthers are longer than filaments. Disc within the stamen ring is well developed and anther lobes enclose the base of the thick filaments. In *C. tagal*, each petal encloses the antipetalous stamen and an adjacent antisepalous stamen; the two stamens remain in the petal under tension enclosed above by the clavate appendages even after anthesis. In both the species, the ovary is semi-inferior, three-carpelled and three-locular with a total of six ovules. Style is slender and terminated into minute separate stigmatic lobes. The stigma stands at the height of the stamens. In *C. tagal*, disc within the stamen ring is well developed and anther lobes enclose the base of the thick filaments.

The mature buds open during 04.30–11.00 h in *C. decandra* and during 16.30–18.00 h in *C. tagal*. In both, the calyx lobes separate at anthesis and diverge to expose the petals. In both species, anther dehiscence occurs at anthesis. In both the stigma attains receptivity on the second day and remains receptive up to six days. However, in *C. tagal*, peak receptivity occurs from third to fifth day; the period of quick release of bubbles from the stigma on hydrogen peroxide application was taken as the duration of peak stigma receptivity. During this period, the white petals turn red gradually from the top to the base. Nectar is produced in trace amount in *C. decandra* but it is 5.65 ± 1.0 µL per flower in *C. tagal*. In *C. tagal*, the nectar sugar concentration is 35–50% and the common sugars include fructose, sucrose and dextrose with the first relatively more dominant. The nectar contains 12 amino acids which include tyrosine, glycine, methionine, proline, lysine, aspartic acid, glutamic acid, serine, cysteine, alanine, threonine and arginine. Of these, glycine, serine, cysteine, alanine and threonine are relatively dominant. Amino acids such as phenylalanine, valine, leucine, iso-leucine, tryptophan and histidine were not found in the nectar. In both the species, the petals and stamens fall off on the seventh day of flower life. The sepals are persistent, become warty and spiny gradually and remain on the plant even after the shedding of propagules.

In *C. decandra*, the fruit set is 1% in bagged flowers, 40% in geitonogamy and 92% in xenogamy. Bud and flower abortion rates are 42% and 31% respectively. Natural fruit set is 15%. Fruit abortion rate is 3%. In *C. tagal*, the fruit set rate in bagged flowers is 3% and 16.3% in open-pollinations. Bud abortion is absent. Flower abortion rate is 42%. Fruit abortion rate is 2%.

The pollinated flowers produce mature fruits in eight weeks in *C. decandra* and four weeks in *C. tagal*. In both, each fruit invariably produces a single seed. In *C. decandra*, fruits are light green, ovoid, conical and blunt apically. In *C. tagal*, fruits are conical by the extrusion of the upper part of the ovary, surface brown and roughened. In both, the fruits are distinct with a five-lobed persistent calyx. The embryo has no dormancy and penetrates through the seed coat and the fruit pericarp and grows to a considerable size into a spindle-shaped hypocotyl structure before dispersal while still attached to the maternal parent. In *C. decandra*, the hypocotyl grows upright and takes three months before detachment from the fruit. It is slender, clearly ribbed, angular, sulcate, 15 cm long and broadened at the lower end. Healthy hypocotyls are entirely green but occasionally purple on one side. A small number of hypocotyls are yellow and drop off prematurely. Visual observations showed that healthy hypocotyls dropped when due, floated in tidal waters and finally settled in areas far away from the mother plant. In *C. tagal*, the cotyledonary yellow cylindrical collar (1cm long) appears from the fruit about 10 days prior to detachment of the hypocotyls. The hypocotyl is 26 cm long, distinctly ridged and hangs downwards. It is initially green, after the development of collar, it shows a gradual colour change to brownish purple from hypocotyl end to plumule. Visual observations indicated that the mature hypocotyls separate from fruit, leaving the latter attached to the mother plant. The detached hypocotyls were found to settle in the vicinity of the mother plant.

Nomia bees (Halictidae) and *Odynerus* wasps (Vespidae) were the foragers of *C. decandra*. They foraged during 10.30–16.30 h, the hourly foraging frequency of individual species (Fig. 1). The bees collected both pollen and nectar while the wasps collected only nectar. In so doing, they contacted the stamens first and then the stigma effecting pollination. During pollen collection, the bees rotated around the flower to collect pollen from the anthers. They took 2–5 seconds to collect the forage from each flower. Their body washings for pollen revealed that they carry 145 to 1,570 pollen grains (Tab. 1) and hence have an important role in pollination. In addition to this pollen, they also carried pollen loads in pollen baskets present on their legs. *Odynerus* wasps while probing the flower for nectar, contacted the stamens and stigma effecting pollination. Their body washings indi-

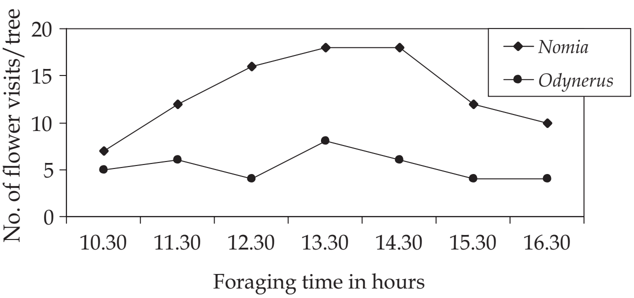

Fig. 1. Hourly foraging activity of *Nomia* bee and *Odynerus* wasp on *C. decandra*

Tab. 1. Pollen carrying capacity of pollinator insects of *Ceriops decandra* and *C. tagal.*

Insect species	Sample size	Range	Mean ± S.D.
		C. decandra	
Nomia sp.	10	145–1570	1132 ± 414
Odynerus sp.	10	80– 540	330 ± 59
		C. tagal	
Chrysomya megacephala	10	79– 147	112 ± 21
Apis cerana indica	10	231– 413	320 ± 68
Apis florea	10	230– 406	310 ± 54

cated the presence of pollen grains ranging from 80 to 540 (Tab. 1). Both bees and wasps frequently moved between trees of *C. decandra* in quest of more forage and this inter-tree movement was considered important for cross-pollination.

In *Ceriops tagal*, the flowers were tripped by the honeybees, *Apis cerana indica* and *A. florea* and the fly, *Chrysomya megacephala* during daytime. Honeybees foraged for pollen and nectar occasionally while the fly foraged for the nectar consistently until the floral source was exhausted (Fig. 2). All the three species while probing for nectar caused the violent release of stamens from the petals. In effect, the pollen from the already dehiscent anthers was ejected forcibly and deposited on the underside of the foraging bee or fly. Body washings revealed the presence of pollen grains ranging from 231 to 413 per bee and from 79 to 147 per fly (Tab. 1). In case of bees, they also carried pollen loads in pollen baskets on their legs. A single foraging visit of the bee or fly did not result in the explosion of all five petals. The honey bees were found to concentrate principally on *B. gymnorhiza* and *A. corniculatum* while the fly species exclusively on *C. tagal.*

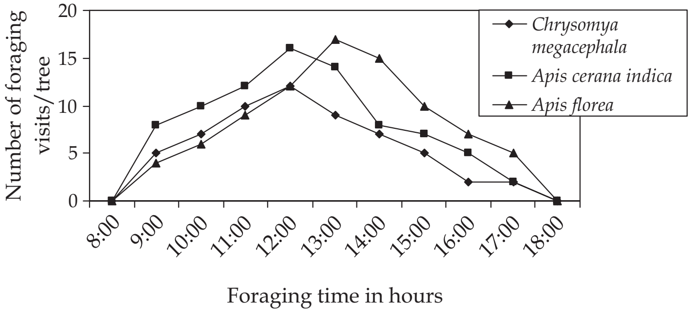

Fig. 2. Hourly foraging activity of insects on *Ceriops tagal.*

The explosion of petals in open flowers of *C. tagal* was also triggered by the action of wind. As the plant grows in the seaward zone, high winds are characteristic of the site, as our experience substantiated. Of the twenty four flowers observed, four flowers exhibited petal explosion triggered by wind action indicating that 16.6% of flowers may achieve pollination by wind action. Neither in such flowers did the explosion of all five petals take place at one time.

Discussion

Ceriops decandra is a year-long bloomer with alternate flowering and fruiting phases whereas *C. tagal* is strictly a winter bloomer with fruit and hypocotyl maturation during summer season. In *C. decandra*, the floral characteristics suggest a simple floral mechanism. The short basal hairs of petal edges have no evident function in *C. decandra* but these hairs are well developed and help to propagate explosive pollen release effectively in the fragrant flowers of *C. tagal* in which petal-stamen configuration is elaborate and specialized (Juncosa and Tomlinson 1987). Also, petal clavate appendages in *C. decandra* have abundant xylem elements with a significant reservoir of water and hydathodes at or near the termini; they have functional significance for flower function under extreme water pressure deficits during the day in mangrove swamps. The abundant xylem is absent in petal appendages in *C. tagal* and *Kandelia candel*, which are pollinated at night, or early in the morning (Juncosa and Tomlinson 1987). Therefore, the abundant xylem and hydathodes and their function in petal appendages of *C. decandra* suggest that the latter is adapted for pollination during the day.

In *Ceriops tagal*, the floral characteristics suggest an elaborate and specialized floral mechanism. The petals require a delicate external touch for the explosive release of stamens. The helically coiled hairs at the lower margins of the petals help to propagate explosive pollen release effectively (Juncosa and Tomlinson 1987). The petal clavate appendages lack hydathodes and abundant xylem which are characteristically present and have a role in flower function under extreme water pressure deficits during the day in *C. decandra* (Juncosa and Tomlinson 1987). Such a state may make appendages very light and provide necessary trigger for petal explosion by delicate touch by the forager in *C. tagal*.

Trigonid bees and small insects usually visit *C. decandra* flowers (Juncosa and Tomlinson 1987). Wasps and flies have been previously found to be suitable for pollination in *C. decandra (*Tomlinson 1986). In the present study, *Nomia* bees and *Odynerus* wasps were consistently frequent pollinators of *C. decandra* flowers. Their foraging frequency and efficiency together characterize them as prime pollinators (Vazquez et al. 2005). Further, the anthesis process is gradual and the accumulation of new flowers with pollen and nectar begins to appear from late morning. Hand-pollination tests show that it is an obligate outcrosser. The protandry, the long period of stigma receptivity and long flower life substantiate this; pollination by bees and wasps favours outcrossing (Tomlinson 1986). The pollen recovered from the body washings of these foragers suggests that the latter effect pollination. The commonness of *C. decandra* at the study site provides ample opportunities for out-crossing effectively and the genetic variation thus achieved would permit the species to survive well in the harsh mangrove environment.

Night-flying insects are probable pollinators in *Ceriops tagal* (Tomlinson 1986). Moths visit the flowers for nectar and bees may also visit during daytime. In this study, we suggest that characteristics such as the absence of nectar guides, and tubular corolla, beginning of nectar secretion prior to anthesis, moderate nectar volume with high sugar concentration having the dominance of hexose sugars, and shallow nature of flowers are suitable for foraging by short-tongued bees and flies (Baker and Baker 1983, Cruden et al. 1983). *Apis* bees and *Chrysomya* flies in terms of their foraging efficiency and frequency are the prime pollinators (Vazquez et al. 2005). *Chrysomya* flies frequent the flowers of *C. tagal* daily effecting pollination but they have limited pollen transport capacity; this however, is compensated by their numbers and could bring about substantial geitonogamy and xenogamy (FAEGRI and VAN DER PIJL 1979). The close proximity between trees of *C. tagal* at the study site also facilitates xenogamy. Pollination also occurs sporadically in nature due to wind action.

Amino acids are the second most abundant class of compounds after sugars to be found in nectar (GARDENER and GILLMAN 2002). Their concentrations in nectars are considerably lower than sugar concentrations. But even the slightest concentrations are important nutritionally and also contribute to the »taste« of the nectar (BAKER and BAKER 1983). In this context, the floral nectar in *C. tagal* plays a crucial role in adding taste and supplying certain amino acids to both honeybees and flies.

Both species of *Ceriops* show a mixed mating system with cross-pollination as the principal mode. *C. tagal* with a small number of individuals at the study site can produce offspring with autogamy if it fails to attract potential and adequate pollinators. *C. decandra* shows a high percent of bud and flower abortion while in *C. tagal*, there is no bud abortion but it displays a high percent of flower abortion. The bud or flower abortion could be due to defective nature of the flowers and also to facilitate adjustment of the available resources to growing healthy fruits and seedlings in order to prevent premature fruit abortion. In both species, fertilized flowers resort to ovule abortion and always only one ovule produces seed as against the actual number of six ovules per flower; this may enable the plant to save resources and use them to produce 1-seeded viable fruits. A few propagules in both species lack green pigment, and have been referred to as »albino« forms (ALLEN and DUKE 2006). These propagules are non-viable, cannot photosynthesize and die after depleting reserves if settled in the habitat. The hypocotyl grows upward in *C. decandra* in which the flowers are sessile while in *C. tagal*, it grows downward which seems to be because of stalked flowers and the greater weight of the hypocotyls. This is an important field characteristic feature to distinguish *C. tagal* from *C. decandra*. In *C. tagal*, the cotyledonary yellow cylindrical collar emerges from the fruit about 10 days prior to the detachment of the hypocotyl while this structure is entirely absent in *C. decandra*.

C. tagal with epigeal seed germination, elongated and pointed hypocotyls with straight curvature (CLARKE et al. 2001) fall freely from the mother plant and plant themselves into the mud at the same site during low tide period. The hypocotyls if fallen during high tides float to another site for settlement. But, field studies do not show settlement of hypocotyls away from the mother plants suggesting that *C. tagal* uses self-planting strategy only. This is further substantiated by MCGUINNESS (1997) who also reported that hypocotyls of *C. tagal* in northern Australia dispersed very short distances. Therefore, the study suggests that *C. tagal* in an undisturbed and human-free site is almost unable to add new plants. In *C. decandra*, the fallen hypocotyls float and settle in different disturbed and undisturbed areas far away from the mother plants. This type of settlement suggests that *C. decandra* uses stranding strategy for establishment.

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