

Reproductive Strategy of *Aegiceras corniculatum* L. (Blanco.) - A Mangrove Species, in MNP&S, Gujarat, India

Richa Pandey¹ & C. N. Pandey¹

¹ Gujarat Forest Department, Gujarat, India

Correspondence: Richa Pandey, Gujarat Forest Department, Gujarat, India. E-mail: richa81181@yahoo.co.in

Received: March 13, 2013 Accepted: October 6, 2013 Online Published: October 18, 2013

doi:10.5539/jps.v3n1p35

URL: <http://dx.doi.org/10.5539/jps.v3n1p35>

Abstract

Mangroves occur in the tropical and subtropical inter-tidal regions of the world. Owing to their locations, they are expected to have a reproductive strategy which can facilitate generalized pollination. The present work has examined the floral biology, breeding system, pollinator resource and their efficiency, and the reproductive strategy of *Aegiceras corniculatum* L. (Blanco) at three islands (three populations) in Marine National Park and Sanstuary (MNP&S), Gulf of Kachchh, Gujarat, India. The temporal relations in the floral processes such as anther dehiscence, stigma receptivity and nectar secretion were studied and the results were juxtaposed to have comprehensive view. The floral life is very long (21 days) and the pace of floral transformation varies with the floral process. Significant diurnal variations in the stigma receptivity and nectar secretions influence the pollinators' availability during different periods of the day. All the three breeding systems are present indicating occurrence of autogamy. However, strong protandry reduces its possibility to a significant level. Further, the asynchrony in the flowering processes at inflorescence level and the foraging behavior of pollinators increase the possibility of geitonogamy. The reproductive strategy of the plant is inclined towards cross pollination with keeping some possibility of self-pollination.

Keywords: mangrove, *Aegiceras corniculatum*, floral biology, pollination biology, stigma receptivity, nectar, pollinator, India

1. Introduction

1.1 Floral Biology- A Brief History

Though floral biology has attracted biologists since eighteenth century, the most fundamental and comprehensive observations were made by Sprengel (1793) who had successfully explained floral biology of 461 angiosperms (with 1 117 illustrations) in terms of floral transformations, functions, fitness, guides, rewards and its association with pollinator resource, determining the type and efficiency of breeding systems. Contrarily, Kölreuter (1761-1766), was of the view that the beauty of flowers had nothing to do with pollination. Willdenow (1802) had supported Sprengel's view while many contemporary workers such as Goethe (1790), Meyer (1953) and Henschel (1820) rejected it and, therefore, it remained in oblivion for decades. Darwin (1888) has rebound Sprengel's philosophy. Thereafter, evolution of plant breeding systems, their efficiency and the regulatory factors have gain enormous attention of biologists (Vogel, 1996; Richards, 1997). However, much of such works were confined to territorial species and very few addressed intertidal species such as mangroves.

1.2 Biology of Mangroves

Mangroves represent the intertidal tropical and sub-tropical communities and the plant component thereof (Tomlinson, 1986). The long distant dispersal of their propagules, largely through water, play important role in their geographical distribution and high inter-population genetic diversity (Geng et al., 2008). Owing to their unique habitat and physiological characters, majority of works pertained to their floristic diversity (Tomlinson, 1986; Rajgopalan, 1987; Banerjee, Shashtri, & Nayar, 1989; Banerjee, Rao, Shashtri & Gosh, 2002; Debnath, 2004; C. N. Pandey & R. Pandey, 2009), ecology (Odum, McIvor, & Smith III, 1982; Tomlinson, 1986; Kathiresan & Bingham, 2001; Ellison, 2008; Morrissey et al., 2010), seed dispersal (Yamashiro, 1961; Steinke, 1986; Clark, 1993; McGuinness, 1997; Stocken et al., 2013) and genetics (Lakshmi, Rajalakshmi, Parani, Anuratha, & Parida 1997; Maguire, Saenger, Baverstock, & Henry, 2000; Lakshmi, Parani, & Parida, 2002; Melville & Burchett, 2002; Kado et al., 2004; Nagrajan, Pandiarajan, Krishnmoorthy, & Sophia, 2008; Homer,

2009). Much less studies have been carried out on the floral biology and reproductive ecology of mangroves (Tomlinson, Primack, & Bunt, 1979; Duke, Bunt & Williams, 1884; Juncosa & Tomlinson, 1987; Steinke, 1988; Aluri, 1990; Coupland, Paling, & McGuinness, 2005; Ghosh, Gupta, Maity, & Das, 2008; Almazol & Cervancia, 2013).

1.3 Reproductive Phenology of Mangroves

Spatial and temporal variations in the reproductive phenology of mangroves are reported (Duke, 2006). *K. candel* has been reported to take about nine months to complete the reproductive cycle with distinct flowering and fruiting peaks (Kamruzzaman, Sharma, & Hagihara, 2013). Day length, wind speed, mean air temperature and monthly rainfall had shown strong correlation with vegetative and reproductive cycles of *K. candel* (Kamruzzaman et al., 2013). Further, salinity and air vapor pressure deficit have been found to trigger flowering in *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia germinans* in the neotropical region (Sánchez-Núñez & Mancera-Pineda, 2011). The reproductive phase continues throughout the year in *Aegiceras corniculatum*, *Ceriops tagal* and *Rhizophora mucronata*, at western coast of India however, their flowering and fruiting show distinct temporal and spatial variations (C. N. Pandey & R. Pandey, 2010a; C. N. Pandey, R. Pandey, & Jain, 2010b; R. Pandey & C. N. Pandey, 2013a).

1.4 Floral Biology and Pollination in Mangroves

Reproductive biology of many mangroves have been examined (Elliot, Edward, & Godfrey, 1996). Some mangroves species such as *Avicennia* (Clarke & Myerscough, 1991; Solomon Raju, Rao, Kumar, & Mohan, 2012; Nadia, Menezes & Machado, 2013), *Bruguiera* (Davey, 1975; Noske, 1993; Nagrajan et al., 2008; Kamruzzaman et al., 2013), *Ceriops* (Solomon Raju et al., 2006; Nagrajan et al., 2008; Solomon Raju, & Karyamserry, 2008, Pandey & Pandey, 2010a), *Rhizophora* (Nagrajan et al., 2008; C. N. Pandey & R. Pandey, 2010a; Ghosh & Chakraborti, 2011; Seetharaman & Kathiresan, 2011), *Laguncularia* (Landry & Rathcke, 2007), *Kandelia* (Sun, Wong, & Lee, 1998), *Aegiceras* (Aluri, 1990; Clark, 1995; Ge & Sun, 1999; Lieu & Hong, 2004; Pandit & Choudhury, 2001; R. Pandey & C. N. Pandey, 2013a), *Scyphiphora hydrophyllacea* (Almazol & Cervancia, 2013), *Xylocarpus granatm* (Almazol & Cervancia, 2013) and *Sonneretia* (Pandit & Choudhury, 2001) have been examined for different aspects of reproductive biology such as population structure, floral biology, breeding systems, pollination etc.

1.5 Pollination Biology of Mangroves

Pollination and subsequent reproductive success of plants are subject many factors viz. availability of floral rewards, effective pollinator resource etc. Owing to their remote locations and less availability of pollinator resources, mangroves are considered to have generalized pollination system (Tomlinson, 1986) in which plant utilizes vast spectrum of pollinator resource (ants, butterflies, bees, moths, bats, birds etc.) for its pollination and is generally facilitated by their gregarious flowering to enhance visual attraction (Willson, 1983; Wyatt, 1983; Harder & Barrett, 1996; C. N. Pandey & R. Pandey, 2010a; R. Pandey & C. N. Pandey, 2013b). However, many times it leads to high inbreeding, the cause of low intra-population genetic diversity (Geng et al., 2008). Pollen grains and nectar are considered the most effective rewards for (floral visitors) pollinators. Azuma, Toyota, Asakawa, Takaso and Tobe, (2002) have examine floral scent of eight mangrove species and concluded that the chemical composition of floral scents can be correlated with floral morphology and pollinators. Variations in the pollinator availability and their efficiency have been reported for three mangrove species in the neotropical (Sánchez-Núñez & Mancera-Pineda, 2012) and tropical regions (C. N. Pandey & R. Pandey, 2010a; R. Pandey & C. N. Pandey, 2013b).

1.6 *A. corniculatum* - The Selected Species

The genus *Aegiceras* initially placed in Myrsinaceae, however, latter it was kept in the family Aegiceraceae (Tomlinson, 1986). Two other genera of this family *Ardisia* and *Myrsine* are reported from mangrove habitats (Tomlinson, 1986; Debnath, 2004; Naskar, 2004). The genus *Aegiceras* is represented by two species i.e. *A. corniculatum* Blanco and *A. floridum* (Tomlinson, 1986). *A. corniculatum* is an evergreen tree or shrub, distributed over Ceylon, South China, Hong Kong, Malaysia, Philippines, New Guinea and tropical Australia (Tomlinson, 1986). In India, *A. corniculatum* is distributed on the east coast, the west coast and in the islands of Andaman and Nicobar (Rajgopalan, 1987; Banerjee et al., 1989; Debnath, 2004; Naskar, 2004). In the state of Gujarat (located on the west coast of India), it is reported from mangrove forests of the Marine National Park and Sanstuary, Gulf of Kachchh, Jamnagar and from South Gujarat regions (GEER, 2000; C. N. Pandey & R. Pandey, 2009; C. N. Pandey & R. Pandey, 2010a).

Comprehensive understanding about the reproductive biology and pollination ecology is the pre-requisite for *in*

situ conservation of any plant species. The floral biology of this species has been examined in many mangrove ecosystems of the world (Clark, 1995; Ge & Sun, 1999; Lieu & Hong, 2004) including India (Aluri, 1990; Pandit & Choudhury, 2001; R. Pandey & C. N. Pandey, 2013a). However, it has not been studied on the west coast of India, specifically in Gujarat. In spite of gregarious flowering, the seed setting and natural recruitment of this species are very low in the mangrove forests of Marine National Park and Sanctuary, Gujarat. Floral biology and availability of efficient pollinators play very important role in reproductive success of any species. It also influences the reproductive strategy of the species; however, these aspects have not been studied for this region. In order to fill this information gap, the present work has examined the floral biology, pollinator efficiency of *Aegiceras corniculatum* L. (Blanco), and attempted to outline its reproductive strategy in Marine National Park and Sanctuary, Gulf of Kachchh (GOK), Gujarat, India.

2. Materials and Methods

2.1 Study Period and Study Area

The study was carried out during March 2007 to May 2009 at the three islands i.e. Pirotan, Patthapir and Sanada of Marine National Park, located at the Southern part of Gulf of Kachchh, Gujarat, India. Pirotan is located between 22°35'849" North and 69°57'486" East. Patthapir is located between 22°31'838" North and 69°56'187" East. Sanada is located between 22°34'084" North and 69°57'374" East. In addition to *Aegiceras corniculatum*, three more mangrove species- *Ceriops tagal*, *Avicenna marina* and *Rhizophora mucronata* - are found at these islands. Among mangrove associates, *Salvadora persica* L. *Salicornia brachiata* Roxb., *Suaeda nudiflora* Roxb., *Suaeda monoica* Forssk. Ex. Gmel., *Cyperus rotundus* L. subsp. *Rotundus* and *Ipomoea pes-caprae* (L.) R. Brown, etc. are most common. Human presence (except for ecotourism and management) is contained due to being located in Marine National Park. Further, soil is predominantly clayey and the tidal amplitude is high in the area which averages around 5-6 meters leading to partial or complete submergence of mangroves. Being in tropical region, three definite seasons prevail here (Summer: March to mid June, Rains: mid June to September, winter: October to February).

The floral biology has been studied in terms of floral transformations, floral processes (viz. anthesis, anther dehiscence, stigma receptivity, nectar secretion). Further, foraging behavior and pollen load on the body of floral visitors were studied for their pollination efficiency. For this, the present work has examined the major pollinators of *A. corniculatum* which were reported by Pandey and Pandey (2013b) for the same region (Table 3).

2.2 Floral Transformations

A total of 52 buds of St-1 (Table 1) were marked and observed daily at regular intervals (8.00 hrs, 12.00 hrs and 17.00 hrs) till they attained the maturity of St-10. During each observation, the floral stage, ongoing floral process and the morphological characters were noted.

Table 1. Morphological details of ten floral states of *A. corniculatum*

Floral stages	Morphological details
St-1	Matured bud without loose petals
St-2	Separation of petals on their lateral margin/s
St-3	Freshly opened flower having anthers without any slit
St-4	Flower with bright white petals, anther/s having slits
St-5	Flower with bright white petals, dried anther/s
St-6	Flower with petals turned off-white, anther lobes brown and twisted
St-7	Flower in which at least one anther shed off (senescence of anthers started)
St-8	Flower without petals and anther (petal and anther senescence completed), style bright white
St-9	Flower with only gynoecium, style turned light pink
St-10	Fruit/Flower with only gynoecium present, style turned prominently pink

2.3 Stigma Receptivity

The stigma receptivity was examined by conducting five experiments:

- *in vitro* examination of the stigma receptivity
- *in vivo* examination of the stigma receptivity
- pollination success of different floral stages
- diurnal variation in the stigma receptivity
- type of stigma (wet or dry)

2.3.1 *In Vitro* Examination of Stigma Receptivity

A total of 1000 floral samples (100 of each floral stage) were examined as per Dafni, (1997) and Dafni and Maues (1998). It works on the principal that the receptive stigma releases CO₂ when it comes in contact with H₂O₂. Further, the degree of receptivity of each floral stage with receptive stigma was examined in terms of number of bubbles of CO₂ it released when it comes in contact with H₂O₂ (Table 2).

Table 2. Degree of receptivity of stigma of different floral stages

Degree of Receptivity	No. of bubbles release	Category allotted
Maximum	More than 5	A
Moderate	< 2, 5 >	B
Minimum	< 2	C
Absent	0	O

For eliminating the subjectivity and ambiguity about the degree to which the categories A, B and C were different from category O, 't test' was conducted treating the Category O as the "control". It has been applied to three pairs of data viz. O-C, O-B and O-A. For the purpose of the t test, the following Null hypothesis was adopted each time.

H_0 : The category under examination (category C, B or A) is different from the Category O

H_1 : The category under examination (category C, B or A) is not different from the Category O

Of the three categories (A, B and C), those which were found statistically not different from category O were clubbed together as single group - Group N (floral stages with significantly non-receptive stigma). Those categories which were found significantly different from group O were clubbed together and treated as Group R (floral stages with significantly receptive stigma).

2.3.2 *In Vivo* Examination of Stigma Receptivity

The stigmatic surfaces of different floral stages were examined for the number of non-germinated pollen grains and germinated pollen grains as per Johansen (1940). A total of 200 samples (20 of each floral stage -Table 1) were examined. The observed numbers of pollen grain on the stigma of different floral stages were categorized into three groups as follows.

Category X: Pollen grain without enlarged germ pores or pollen tubes (non-germinated pollen grains)

Category Y: Pollen grain with enlarged germ pores but without pollen tube

Category Z: Pollen grain with pollen tube (germinated pollen grains)

The percent distribution of pollen grains belonging to category Y and Z have been juxtaposed against the percent distribution significant stigma receptivity for *in vivo* examination of different floral stages.

2.3.3 Pollination Success

The ratio of the number of pollen tube formation in the style to the total pollen grain load on the stigma (Alonoso & Herrera, 2008) was studied as per the Equation (1). A total of 120 samples, spread over six floral stages (St-4, St-5, St-6, St-7, St-8 and St-9) were examined.

$$\text{Pollination Success} = \frac{\text{No. of Pollen tubes formation in the style}}{\text{Total pollen grain load on the stigma}} \quad (1)$$

2.3.4 Diurnal Variation in the Stigma Receptivity

The *in vitro* experiment of stigma receptivity was conducted during three time zones T1 (8:00 to 12:00 hrs), T2

(from 12:00 to 16:00 hrs) and T3 (from 16:00 to 19:00 hrs). This experiment was conducted on four floral stages viz. St-6, St-7, St-8 and St-9. A total of 300 samples (25 floral specimens of each selected floral stage) examined in each of the three time zones for diurnal variation, if any.

2.3.5 Type of Stigma

The stigma of all the ten floral stages were collected, preserved in 70% alcohol and examined under scanning electron microscope for stigmatic exudates, if any.

2.4 Nectar Secretion

Under this section, following experiments were conducted:

- structure and location of floral nectaries
- availability of nectar in different floral stages
- diurnal variation in nectar availability
- chemical composition of nectar

2.4.1 Structure and Location of Floral Nectaries

The floral specimens were collected and processed (Johansen, 1940) for light microscopy. Some samples were preserved in 70% alcohol and observed under scanning electron microscope.

2.4.2 Availability of Nectar in Different Floral Stages

This experiment did not examine nectar production per flower per day, as the flowers were not bagged to avoid nectar collection by foragers. In fact, it attempted to examine nectar availability during different periods of the day. The presence of nectar was examined by putting a capillary tube at the source of nectar and holding it for 10 minutes and subsequently the volume of nectar was calculated. For each specimen, separate capillary tubes were taken. Further, each individual examined for nectar secretion was different. Since the senescence of petals and stamens takes place during St-8 (Table 1), nectar availability stops from St-8 onwards. Hence, the floral stages prior to St-8 (viz. St-1 to St-7) were examined for nectar secretion.

2.4.3 Diurnal Variation in Nectar Secretion

A total of 70 floral specimens (10 specimens of each floral stage St-1 to St-7) were examined during each time zone (T1, T2 and T3). Hence, 210 floral samples were examined.

2.4.4 Chemical Composition of Nectar

Thin Layer Chromatography (TLC) method was used to examine the sugar and amino acid components of nectar.

2.5 Floral Morphometry

It aimed to examine the physical separation between stigma and anther and also the rate of growth of gynoecium and androecium. The buds and flowers of four floral stages i.e. St-1, St-3, St-4 and St-8 were selected and a total of 120 samples (30 for each stage) were examined. The measurements were taken using a dissecting microscope and the measuring equipment or scale which could read up to 1/10th of the millimeter. Thus, the least count for linear measurements was 0.1mm. Further, the lengths of anther filament, anther lobes, ovary and style were measured. In addition the width of anther lobes were also taken.

2.6 Pollination Biology

Pandey and Pandey (2013b)* have identified major floral visitors of *A. corniculatum* and examined their spatial and temporal major floral visitors in GOK. The present study has taken it further and examined:

- Foraging behavior of major floral visitors
- Pollination efficiency of major floral visitors
- Major floral visitors : pollinators or non pollinators?

2.6.1 Foraging Pattern of Major Floral Visitors

A total of 21 species of floral visitors were observed for their foraging pattern in terms of their movement across the inflorescences, average foraging duration, physical contact of their body parts with the reproductive parts of flower (stigma/anther), foraging location/s (nectar/anther), associated floral visitors (if any). In the case of diurnal floral visitors, direct observations have been made. However, in the case of nocturnal floral visitors, video documentation has been carried out.

Table 3. Details of observations made about foraging pattern of major floral visitors*

Group Name	Scientific Name/Family/Unidentified	Symbol	Family	No. of observations
Bees	<i>Apis dorsata</i>	Hb1	Apidae	186
	<i>Apis florea</i>	Hb2	Apidae	181
	<i>Lasioglossum</i> sp.	Hb3	Halictidae	96
Birds	<i>Acrocephalus stentoreus</i>	Bi1	Muscicapidae	42
	<i>Nectarinia zeylonica</i> L.	Bi2	Nectariniidae	35
	<i>Zosterops palpebrosus</i>	Bi3	Zosteropidae	107
Ant	<i>Crematogaster brunnea contemta</i>	A	Formicidae	332
Bumble Bees	<i>Scolia aureipennis</i>	BB1	Scoliidae	50
	<i>Sphex umbrosu</i>	BB2	Sphecidae	29
	<i>Xylocopa aestuans</i>	BB3	Apidae	100
Butterfly	<i>Anaphaeis aurota</i> F.	Bu1	Pieridae	29
	<i>Tirumala septemtrionis</i>	Bu2	Nymphalidae	18
	<i>Vanessa cardui</i>	Bu3	Nymphalidae	37
	Lichniidae	Bu4	Lichniidae	28
	Pieridae	Bu5	Pieridae	24
Mosquito	Unidentified	Ms	Culicidae	28
Moth	<i>Achaea janata</i>	M1	Noctuidiae	21
	<i>Crocidolomia botalis</i>	M2	Crambidae	21
	<i>Utethesia latrrix</i>	M3	Arctiidae	24
	<i>Helicoverpa armigera</i>	M4	Noctuidiae	24
	<i>Spodoptera litura</i>	M5	Noctuidiae	21
Total observations				1433

2.6.2 Efficiency of Major Floral Visitor/Pollinators

The major floral visitors were examined for the pollen grain/s of *A. corniculatum* on their body. The pollen grains of other existing flora were also collected to cross referred and ensure whether the pollen grains on the body of the floral visitors belonged to *A. corniculatum* or not. The floral visitors observed with pollen grain/s of *A. corniculatum* on their body were categorized as pollinators. The pollinators were further categorized as most efficient, moderately efficient or least efficient based on the pollen grain load on their body (Table 4).

Table 4. Categorization of pollinators based upon the pollen grain on their body

Category	Average pollen grain load on body
Most efficient	> 50 pollen grains
Moderately efficient	21-50 pollen grains
Least efficient	01-20 pollen grains

The pollen load on the body of butterflies, moths and birds could not be examined. In such cases, if their foraging behaviour suggest them as pollinator, have been treated as potential pollinators.

2.7 Breeding Systems

For autogamy, matured buds (St-1) were bagged individually in butter paper bags. A second set (Table 5) of matured buds (St-1) were emasculated and subsequently hand pollinated by the pollen grains of different flowers

of the same plant (geitonogamy) and bagged with butter paper bags. For examined the occurrence of xenogamy, a third set of matured buds (Table 5) were emasculated and pollinated by pollen grain of different flowers of different plant and bagged with butter paper bags. Observations were taken fortnightly till the survived buds achieve fertilization successes indicated by morphological characters (Table 5).

Table 5. Details of breeding experiments

Breeding mechanism	No. of samples	Frequency of observation	Morphological character indicating fertilization success
Autogamy	70		
Geitonogamy	371	Fortnight	Senescence of petals, anthers and dark pinkish coloration of the style
Xenogamy	225		

2.8 Reproductive Strategy

This has been outlined based on the findings of sub sections (2.2, 2.3, 2.4, 2.5, 2.6 and 2.7).

3. Results

3.1 Floral Transformations

A matured bud of *A. corniculatum* takes 525 hrs (about 21 days) to transform to the stage of seed setting St-10 (Table 6). During this period, a flower remains open (St-3 to St-6) for 38 hrs prior to stamen and petal senescence and for 277 hrs (St-7 to St-9) after the stamen and petal senescence (Figure 1). The anther dehiscence takes place during St-4 which last for about 10 hrs. Among the ten floral stages, St-8 was found to be the longest followed by St-9. On the contrary, the St-4 was found to be the shortest floral stage. The durations of St-2, St-3 and St-4 were similar.

Table 6. Floral transformations and floral processes of *A. corniculatum*

Floral stage	Range of life span (hrs) (Avg. life \pm confidence interval at 95% level)	Floral processes	Pace of transformation after completion of anthesis -taking St-2 as zero
St-1	23.8 \pm 5.08	Matured bud	Day 0
St-2	8.5 \pm 2.78	Duration of anthesis	
St-3	11.7 \pm 3.43	Duration prior to anther dehiscence	Day 1
St-4	9.4 \pm 2.52	Anther dehiscence (pollen presentation period)	Day 1
St-5	15.7 \pm 2.29	Drying of anthers	Day 2
St-6	39.9 \pm 8.30	Shrinkage of the petals	Day 4
St-7	17.0 \pm 3.60	Senescence of petals and stamens	Day 5
St-8	226.3 \pm 36.1		Day 13
St-9	174.7 \pm 25.59	Predominantly female flower	Day 21

3.2 Stigma Receptivity

The stigma is surrounded by 5 anthers (Figure 1) and is wet type (Figure 2 A) due to the presence of stigmatic secretions reported during St-7, St-8 and St-9.

Figure 1. Floral transformation of *A. corniculatum* and the ten floral stages

Table 7. Percent Distribution of significant stigma receptivity, pollen grains of Category Y and Z

Floral Stage	No. of floral samples		Percent Distribution of				
	Group R	Group N	Significant stigma receptivity (SR)	Total grains stigma	Pollen on	Pollen grains of Category Y	Pollen grains of Category Z
St-1	100	0	0	0	0	0	0
St-2	100	0	0	0	0	0	0
St-3	100	0	0	0	0	0	0
St-4	85	15	5.2	25	0	0	0
St-5	73	27	9.40	25	0	0	0
St-6	67	33	11.49	16	12	0	0
St-7	33	67	23.34	14	34	2	0
St-8	26	74	25.78	18	53	96	0
St-9	32	68	23.69	3	1	2	0
St-10	97	3	1.04	0	0	0	0
Total	713	287	100	100	100	100	100

3.2.1 *In Vitro* Examination

Significant stigma receptivity is present in seven floral stages i.e. St-4 to St-10 (Group R) and is absent in three floral stages St-1, St-2 and St-3 (Group-N). It increases from St-4 onwards and attains high values during St-7 to St-9 (with peak during St-8) and dramatically drops down in St-10. The maximum samples belonging to Group R were found in the floral stage St-7, St-8 and St-9 (Table 7). The percent occurrence of significant stigma receptivity rises sharply in St-7 (from 33% to 67%) and drops dramatically in St-10 (from 68% to 3%).

3.2.2 *In Vivo* Examination

Out of 200 specimens, 80 floral specimens had pollen grains and 120 floral specimens did not have pollen grain on their stigma. Further, of the ten floral stages, pollen grains have not been found on the stigma of St-1, St-2,

St-3 and St-10. The percent distribution of pollen grains belonging to category Y and Z (Figure 2 B) have been juxtaposed against the percent distribution significant stigma receptivity over different floral stages (Table 7).

Pollen grains with enlarged germ pores (category Y) was seen St-6 onwards with peak in St-8. While pollen grains with germ tubes were seen maximum in St-8 (Table 7). The percent occurrence of significant stigma receptivity (*in vitro* method) and the percent occurrence of pollen with enlarged germ pores have been found to be strongly positively correlated ($r = 0.71$). The percent occurrence of significant stigma receptivity and the percent occurrence of pollen with pollen tubes have also been found to be positively correlated ($r = 0.52$). Hence, observations of the *in vitro* experiment are in conformity with those from the *in vivo* experiment. Maximum stigma receptivity is during St-8.

3.2.3 Pollination Success

Germinated pollen grains were absent in St-5 and St-6. Hence, the pollination success was zero during these floral stages. Out of the 20 floral specimens, only one floral specimen was found to have a pollen tube in St-7 and St-9 each. Therefore, the pollination success was found to be 0.1 in these floral stages. The pollination success ranged from 0.0 to 0.5 for stage St-8. The average pollination success was found to be 0.01, 0.15 and 0.04 for St-7, St-8 and St-9 respectively.

3.2.4 Diurnal Variation of Stigma Receptivity

Stigma receptivity is high in the morning and evening hours and is unambiguously low- almost absent (found in < 5% flowers) during the afternoon (i.e. T-2). Thus, *A. corniculatum* has been found to show noticeable diurnal variation in the stigma receptivity. Although the number of flowers with significantly high stigma receptivity is very high in the morning and evening hours in all the four floral stages under examination, it is relative more in evening hours for St-6, St-7 and St-9 and is relatively more in morning hours in St-8.

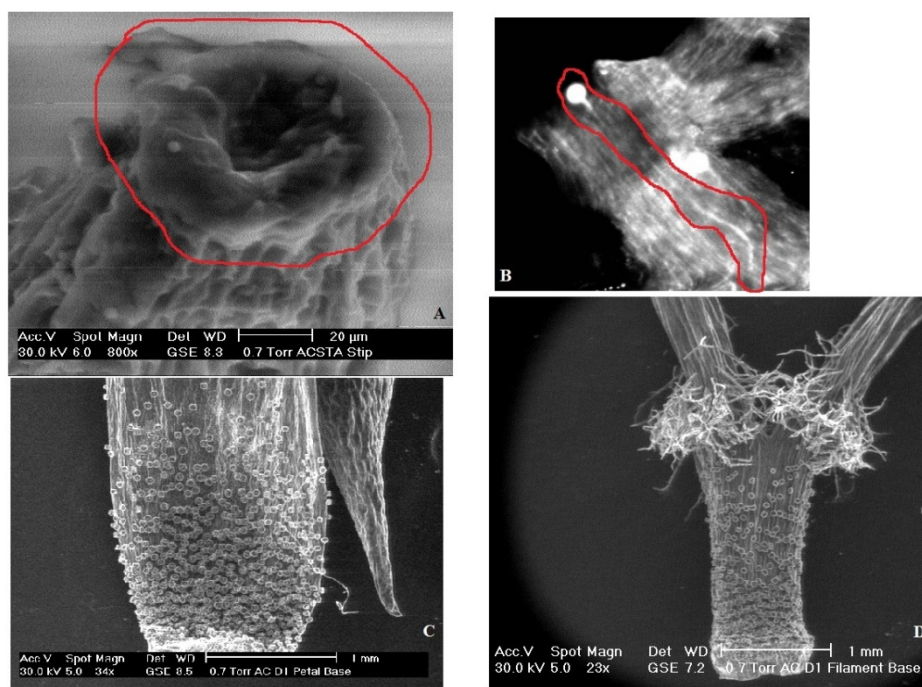


Figure 2. Stigmatic secretion during St-8 (A), Pollen germination and pollen tube growth through stylar canal in Sta-8 (B), Nectaries at base of petal (C) and Nectaries at base of stamen filament (D)

3.3 Nectar Secretion

3.3.1 Floral Nectaries

The floral nectaries, present at the base of the petals (Figure 2 C) and stamen filaments (Figure 2 D), are multicellular and stalked. These nectaries have two major parts i.e. basal stalk and apical head. The stalk is multicellular and composed of 1-5 layers of cells while the head is comprised of single layered 5-10 secretory

cells covered with cuticle at apex.

3.3.2 Availability of Nectar in Different Floral Stages

The presence of nectaries is more at the base of the petal than the stamen filament. The nectar is found in four floral stages St-4 to St-7; and is absent in the rest floral stages i.e. St-1 to St-3 and from St-8 onwards (due to senescence of petals and androecium).

3.3.3 Diurnal Variation in Nectar Availability

The nectar availability is high during morning and evening hrs while very low during the noon period (Table 8). Considering all the 120 flowers, which were examined for nectar availability, the total quantum of nectar was 362.7 mm³. Out of this, the contribution of St-4, St-5, St-6 and St-7 was 104.1 mm³, 62.6 mm³, 98.7 mm³ and 97.3 mm³ respectively. During afternoon, the nectar availability per flower was found to decrease. The low availability of nectar during the afternoon may be partially attributed to the possibility of loss of nectar due to evaporation. However, the trichomes/corona present at the base of the filament (Figure 2 D) of the anther protect the nectar to some extent- from getting evaporated. Therefore, there are only small possibilities of nectar getting evaporated during the afternoon period. It is more likely that the nectar productivity is reduced during the afternoon hours.

Table 8. Nectar availability (mm³) in the various floral stages during different time periods

Sr. No. /Floral age	Morning (T1)				Afternoon (T2)				Evening (T3)			
	St-4	St-5	St-6	St-7	St-4	St-5	St-6	St-7	St-4	St-5	St-6	St-7
1	4.2	3.1	6.0	3.1	1.3	0.0	1.3	0.0	6.3	3.1	1.4	7.4
2	3.1	1.9	5.3	3.1	0.0	2.5	2.8	0.0	6	2.8	3.1	7.5
3	3.5	2.8	5.7	3.5	0.0	0.0	0.0	4.9	6.4	3.5	4.1	6.1
4	3.4	1.8	5.9	3.5	0.0	0.0	0.0	4.2	4.6	3.1	3.9	4.1
5	3.1	2.8	6.0	2.8	0.0	0.0	0.0	0.0	6.2	3.8	5.0	2.5
6	2.8	3.8	6.2	2.5	1.5	0.0	0.0	0.0	5.4	3.0	3.5	4.3
7	3.1	3.3	6.0	3.1	0.0	0.9	0.9	0.0	7.6	3.1	3.5	6.0
8	3.5	1.9	5.7	3.1	0.0	1.2	1.1	9.2	4.1	3.1	2.8	3.8
9	3.5	1.3	6.0	3.1	2.8	0.0	0.9	0.0	6.2	3.1	4.1	3.8
10	3.1	1.7	5.3	3.1	1.0	0.0	0.0	0.0	6.8	4.6	2.5	2.5

In the late evenings, the nectar availability was again high in all the ten specimens of the four floral stages. Interestingly, the nectar availability per flower in the evening hours was found to be slightly higher in St-4 than that of St-5, St-6 and St-7. It may be attributed to the fact that the flower of *A. corniculatum* is white which turns dull white or brown during St-6 and St-7. Further, the nocturnal visitors would be attracted by the bright white flowers of St-4 and not by the dull brown flowers of St-6 and St-7. Therefore, to attract the nocturnal floral visitors, the nectar availability per flower might possibly be higher in St-4 as compared to St-5, St-6 and St-7 during the evening hours. Considering the nectar availability per flower, it was found to be the maximum at St-4 (29%) followed by St-6 and St-7 (27% each) and St-5 (17%).

3.3.4 Chemical Composition of Nectar

The floral nectar shows the presence of four sugars viz. fructose, galactose, maltose and sucrose and two amino acids viz. amino butyric acid and aspartic acid.

3.4 Morphometry

Considering St-1 as the benchmark (Table 9), the growth of the stamen is relatively more during early stage (St-1 to St-3) while that of pistil during latter stages (after St-3) is a morphological manifestation of protandry.

Table 9. Dimensional details (mm) of stamen and pistil at four floral stages

Floral stages	Stamen				Pistil					
	Filament		Anther		Ovary				Style	
			Length	Width						
	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD
St-1	4 to 8	6.7 \pm 0.9	4 to 5	4.3 \pm 0.4	1.5 to 3.5	2.0 \pm 0.3	0.8 to 1.5	1.0 \pm 0.1	8.1 to 10.0	9.0 \pm 1.0
St-3	8 to 12	10.1 \pm 1.2	4 to 5	4.4 \pm 0.4	1.2 to 2.0	1.9 \pm 0.2	1.0 to 1.5	1.10 \pm 0.1	8.0 to 11.0	9.5 \pm 1.0
St-4	9 to 12.5	10.6 \pm 1.0	3.5 to 5	4.2 \pm 0.4	1.0 to 2.0	1.6 \pm 0.4	1.0 to 1.2	1.0 \pm 0.1	9.0 to 12.0	10.6 \pm 0.9
St-8	11 to 14	12.1 \pm 0.8	3.0 to 4.0	3.2 \pm 0.4	1.0 to 1.1	1.0 \pm 0.03	1.0 to 2.0	1.3 \pm 0.4	10.5 to 13.0	11.7 \pm 0.7

SD: Standard deviation.

3.5 Pollination Biology

3.5.1 Foraging Behavior

Birds were seen throughout day with more frequency during late evenings and early morning hrs. Though single individuals were reported, they generally found foraging in groups of 2 to 4 individuals per tree. They visit 4-12 inflorescences per tree in a landing. Further, they also visit the neighboring conspecific trees in one landing. Their foraging duration ranges from 0.05 minutes to 8 minutes with an average of 1.8 minute per inflorescence. All bird species prefer the inner branches. Many times they were found collecting ants as well. Ants are maximum reported foraging on flowers in early morning hrs. They forage in groups of 2 to 5 individual per flower. Ants always search for the nectar and never collect pollen. However, in the process to reach the nectar, they pass through anther and/or stigma (Table 10). Its foraging duration ranges from 0.01 to 10.0 minutes. They prefer to forage on floral stages after St-4 (when nectar secretion initiates). Once ants have entered in the flower, they do not allow any other species (such as bees) to forage on the same flower, even if the later have landed prior. Bees were seen throughout the day. They also forage in groups but they do not disturb other species. Their foraging durations range from 0.01 to 20 minutes with an average of 2 minutes per landing. Once landed on an inflorescence and remained undisturbed, they forage on almost every individual of the inflorescence, irrespective of the floral stage. During initial floral stages, they collect pollen while in latter floral stages, they collect nectar (Table 10). Bumble bees were seen more during morning and noon period. However, only one to two individuals were seen during the sightings. Their foraging duration ranges from 4 seconds to 27 minutes. Per landing, bumble bees were reported to visit one to five inflorescences. While in a single sight, they were seen to visit one to 20 conspecific trees. They were reported to collect pollen as well as nectar (Table 10). Butterflies were found to forage for still shorter durations. They never found foraging in groups. One diurnal and four nocturnal moths were found foraging on *A. corniculatum*.

All the flying floral visitors use the refluxed petals as landing ground. Butterflies hold the corolla cup while collecting nectar. Bees and bumble bees land on petals while birds land on branches. Bees, were never reported sharing an inflorescence with birds.

Table 10. Foraging behaviors of pollinators & potential pollinators

Species symbol*	Observations	Body parts touching				Foraging activity			
		Anther		Stigma		Pollen collection		Nectar collection	
		No.	%	No.	%	No.	%	No.	%
Ant-A	Yes	274	83	12	4	0	0	332	100
	No	52	16	320	96	332	100	0	0
	Unknown	6	1.8	0	0	0	0	0	0
	Total	332	100	332	100	332	100	332	100
Be1	Yes	185	99	179	96	48	26	173	93
	No	0	0	7	4	131	70	12	6
	Unknown	1	1	0	0	7	4	1	1
	Total	186	100	186	100	186	100	186	100
Be2	Yes	178	98	132	73	5	3	181	100
	No	0	0	46	25	176	97	0	0
	Unknown	3	2	3	2	0	0	0	0
	Total	181	100	181	100	181	100	181	100
Be3	Yes	96	100	89	93	68	71	75	78
	No	0	0	6	6	28	29	20	21
	Unknown	0	0	1	1	0	0	1	1
	Total	96	100	96	100	96	100	96	100
Bi1	Yes	42	100	42	100	0	0	00	00
	No	0	0	0	0	42	100	26	38
	Unknown	0	0	0	0	0	0	116	62
	Total	42	100	42	100	42	100	42	100
Bi2	Yes	35	100	35	100	0	0	35	100
	No	0	0	0	0	35	100	0	0
	Unknown	0	0	0	0	0	0	0	0
	Total	35	100	35	100	35	100	35	100
Bi3	Yes	107	100	107	100	0	0	103	96
	No	0	0	0	0	106	99	4	4
	Unknown	0	0	0	0	1	1	0	0
	Total	107	100	107	100	107	100	107	100
BB1	Yes	50	100	50	100	0	0	50	100
	No	0	0	0	0	50	100	0	0
	Unknown	0	0	0	0	0	0	0	0
	Total	50	100	50	100	50	100	50	100
BB2	Yes	29	100	29	100	0	0	29	100
	No	0	0	0	0	29	100	0	0
	Unknown	0	0	0	0	0	0	0	0
	Total	29	100	29	100	29	100	29	100
BB3	Yes	75	75	75	75	20	20	93	93

Species symbol*	Observations	Body parts touching				Foraging activity			
		Anther		Stigma		Pollen collection		Nectar collection	
		No.	%	No.	%	No.	%	No.	%
	No	8	8	8	8	80	80	7	7
	Unknown	17	17	17	17	0	0	0	0
	Total	100	100	100	100	100	100	100	100
Bu1	Yes	29	100	29	100	0	0	29	100
	No	0	0	0	0	29	100	0	0
	Unknown	0	0	0	0	0	0	0	0
	Total	29	100	29	100	29	100	29	100
Bu2	Yes	18	100	18	100	18	100	18	100
	No	0	0	0	0	0	0	0	0
	Unknown	0	0	0	0	0	0	0	0
	Total	18	100	18	100	18	100	18	100
Bu3	Yes	27	73	12	32	0	0	37	100
	No	6	16	21	57	37	100	0	0
	Unknown	4	11	4	11	0	0	0	0
	Total	37	100	37	100	37	100	37	100
Bu4	Yes	28	100	7	25	68	71	28	100
	No	0	0	21	75	28	29	0	0
	Unknown	0	0	0	0	0	0	0	0
	Total	28	100	28	100	96	100	28	100
Bu5	Yes	28	100	18	64	0	0	28	100
	No	0	0	10	36	28	100	0	0
	Unknown	0	0	0	0	0	0	0	0
	Total	28	100	28	100	28	100	28	100

* refer Table 3.

3.5.2 Pollinator's Efficiency

Of the 21 major pollinators (R. Pandey & C. N. Pandey, 2013b), 13 were found pollinators and 8 potential pollinators. Three pollinators were most efficient, two moderately efficient and eight the least efficient (Table 11). The availability and efficiency of floral visitors are summarized at Table 11. Some pollinators and potential pollinators foraging on flowers of *A. corniculatum* could be photo-documented (Figure 3).

3.6 Breeding Systems

All the three breeding mechanisms were found in this species. The fertilization success of autogamy, geitonogamy and xenogamy was 27.14%, 26.15% and 23.11% respectively.

3.7 Reproductive Strategy

A single inflorescence has 8 to 24 individuals which develop asynchronously. Therefore, a single inflorescence may have all floral stages at the same time. The petals are white but they do not have any other colour or pattern which could work as additional guide for the visitors. However, the strong fragrance attracts floral visitors. Due to gregarious flowering, this odour gets diffused in the atmosphere and, therefore, it does not act as a very focused floral guide. Thus, it attracts the visitors to the tree rather a particular flower/inflorescence. After reaching the inflorescence, the visitors hover around it.

The pollen presentation period, St-4, is about 10 hrs which is much prior to stigma receptivity which is the

maximum during St-8 and St-9. Stigma is exposed beyond the senescence of stamens (St-7 to St-9) for 277 hrs. The species keeps a very long period of significant stigma receptivity to receive pollen grains from other flowers after the possibility of self-pollination is ruled out. At these stages, the flower tends to get pollen grains (Table 7) by elongating the style (Table 9) and better exposing the stigma to the pollinators who may be hovering around. Further, nectar secretion initiates during St-4 which attains its peak during St-6 (Table 8) and terminates during St-8. During St-4, the nectar produced is intended to attract pollinators who can take away pollen grains to other receptive flowers because the stigma receptivity in the same flower is extremely low during this stage. However, St-6 onwards, the nectar is meant for attracting pollinators who may bring pollen grains to its receptive stigma. Hence, the temporal pattern of nectar production, much beyond the period of anther dehiscence is also supportive of cross breeding. These facts strongly suggest species favours cross pollination with keeping small possibility of self-pollination.

Table 11. Efficiency of Pollinators

Sr. No.	Species Symbol*	Range of pollen load on body	Average pollen load \pm SE	Category allotted
1	A	0 to 9	2.4 \pm 0.9	Least efficient
2	Be1	3 to 123	60.3 \pm 12.6 SE	most efficient
3	Be2	1 to 200	36 \pm 13.4 SE	moderately efficient
4	Be3	1 to 435	86.6 \pm 43.6	most efficient
5	Bi1	NA	NA	Potential pollinators
6	Bi2	NA	NA	Potential pollinators
7	Bi3	NA	NA	Potential pollinators
8	BB1	3 to 52	22.5 \pm 8.4	moderately efficient
9	BB2	17 to 109	61.7 \pm 20.6	most efficient
10	BB3	6 to 24	16.4 \pm 3.6	Least efficient
11	Bu1	NA	NA	Potential pollinators
12	Bu2	NA	NA	Potential pollinators
13	Bu3	NA	NA	Potential pollinators
14	Bu4	NA	NA	Potential pollinators
15	Bu5	NA	NA	Potential pollinators
16	M1	NA	NA	Potential pollinators
17	M2	NA	NA	Potential pollinators
18	M3	NA	NA	Potential pollinators
19	M4	NA	NA	Potential pollinators
20	M5	NA	NA	Potential pollinators
21	Mo	2 to 14	8 \pm 2	Least efficient

* refer Table 3, NA: Not applicable



Figure 3. Pollinators and potential pollinators foraging on flowers of *A. corniculatum*

4. Discussions and Conclusions

4.1 Floral Biology

The range of individual per inflorescence was found 4-24 with an average of 16 per inflorescence which is in agreement with the findings (20 individuals) of Aluri (1990) indicating gregarious flowering in *A. corniculatum*. In *A. marina*, another mangrove species, individual floral life is 2-5 day while the inflorescence life may go up to 2-5 weeks (Clarke & Myerscough, 1991). *Aegiceras floridum* takes 3 days (Almazol & Cervancia, 2013) and *A. corniculatum* also take 2-3 days (Aluri, 1990) to complete flowering. However, in the present work *A. corniculatum* was found to complete the floral cycle in 21 days on west coast of India. If drying and senescence of petals are taken as indication of termination of floral life, it takes 3-4 days by *A. corniculatum* in GOK. But, even if the petals and stamens have gone, the stigma receptivity has not yet achieved its peak and majority of flowers are yet to be pollinated (Table 7). Thus, the floral life does not complete with the senescence of petals and stamens. In fact, the flower remains open (St-3 to St-6) for 38 hrs prior to stamen and petal senescence (effectively male flower) and for 277 hrs (St-7 to St-9) after the stamen and petal senescence (effectively female flower).

Anthesis was reported during 0500 hrs to 1900 hrs with maximum completion during forenoon period for *A. corniculatum* (Aluri, 1990) while Almazol and Cervancia (2013) found anthesis initiation 0530 onwards with peak during 0900 to 1000 hrs for *A. floridum*. Present work has reported anthesis throughout 24 hrs with maximum peaks during early morning and midnight. Pollen and nectar have been found major floral rewards for many mangrove species (Aluri, 1990). Elliot et al. (1996) have reported 0.28 microliter/flower/day and 0.40 microliter/flower/day nectar from *A. germinans* and *L. racemosa* respectively. Pollen grains are important floral rewards for *A. corniculatum* (Aluri, 1990). Present work has unambiguously found nectar and pollen both as floral reward of *A. corniculatum*. During initial floral stages (till St-4) pollen are the floral reward as the nectar secretion has yet not started. However, nectar is the floral reward from St-4 to St-7. The significant variation in

the nectar availability during morning, afternoon and evening hrs influences the frequency of pollinators and potential pollinators of *A. Corniculatum*, in MNP&S.

Choudhury and Pandit (2001) have reported that the anther and stigma are at the same level. However, this study has found that during the later floral stages, the stigma elevates due to the elongation of the style. Choudhury and Pandit (2001) have also reported simultaneous maturation of anthers and stigma and treated it as a selfing species; however, any observational detail supporting simultaneous maturity of the anther and stigma has not been mentioned. The present research has unequivocally found that neither anther and stigma are at same level nor their maturation are not simultaneous. Aluri (1990) and Pandit and Choudhury (2001) have found *A. corniculatum* a predominantly selfing (autogamous) species. Present study has reported all the three breeding mechanisms in this species; however, the strong protandry reduces the possibility of autogamy to a significant level. Similar observations were made by Clarke and Myerscough (1991) for *A. marina* and reported protandry eliminates the possibility of self-pollination but asynchrony in flowering processes at inflorescence level and the visitation of pollinators favors geitonogamy which is found true for *A. Corniculatum* as well.

4.2 Pollination Biology

The pollination and reproductive biology of mangrove species are expected to differ among the populations. However, very few studies have addressed this aspect (Elliot, 1996; C. N. Pandey & R. Pandey, 2010a). Pollinator dependent reproductive success has been reported in mangrove species (Elliot et al., 1996; C. N. Pandey & R. Pandey, 2010a; Nadia et al., 2013). On the other hand, generalized pollination system is not uncommon for mangroves (Tomlinson et al., 1979; R. Pandey & C. N. Pandey, 2013b). *Laguncularia racemosa* was reported to have the most specialized while *Avicennia germinans* with least specialized pollination (Nadia et al., 2013). Although known as wind pollinated species, insect pollination has been reported in *R. mangle* (Elliot, 1996; Sánchez-Núñez & Mancera-Pineda, 2012) and *R. mucronata* (Pandey & Pandey 2013c). Butterflies (*A. germinans*), wasp (*L. racemosa*) and birds were reported as major pollinators of Bahamas mangroves. Ge and Sun (1999) and Aluri (1990) found that *A. corniculatum* is predominantly pollinator-dependent for fruit setting. Similar observations were made for *Kandelia caldel*, another mangrove species (Sun et al., 1998). Nevertheless, the foraging pattern and asynchrony in the flowering processes within an inflorescence tend to geitonogamy in many mangrove species (Sun et al., 1998; Ge & Sun, 1999) which is in conformity with the findings of present study.

The availability and efficiency of pollinators regulates the reproductive success of a pollinator dependent population. A total of 35 floral visitors of *A. corniculatum* have been documented by Pandit and Choudhury (2001). These 35 floral visitors included 7 nocturnal and 28 diurnal floral visitors. Further, 16 floral visitors belonged to the order Lepidoptera and the rest to Hymenoptera, Coleoptera, Diptera and Passeriformes (Pandit & Choudhury, 2001). However, those floral visitors were neither categorized as pollinators/non pollinators/thieves/robber nor they were examined for their availability and pollination efficiency. On the other hand, Aluri (1990) reported *Trigona* sp. and *Pseudapis oxybeloides* collecting pollens from flowers of *A. corniculatum* which were not found in the present study. Almazol and Cervancia (2013) reported *Xylocopa* spp. and *Apis dorsata* foraging on *A. floridum*. Both of them are reported in the present work.

Pandit and Choudhury (2001) has reported that the members of Lepidoptera dominates among the floral visitors of *A. corniculatum* in Bhitarkanika mangrove forests which is also found in the present work. Three pollinators viz. *Apis dorsata*, *Nectarinia zeylonica* and *Zosterops palpebrosus* were reported in both the studies. Interestingly, Aluri (1990) has found *Apis florum*, *Xylocopa latipes*, *X. pubescence*, *Nectarinia asiatica* and *N. zeylonia* foraging on many mangroves on east coast (Andhra Pradesh) of India but *A. corniculatum*. However, present work has found *Apis florum* and as pollinator and *N. zeylonia* as potential pollinator of *A. corniculatum*. Further, *Xylocarpa aestuans* which was not reported by Aluri (1990) has been found as pollinator of *A. corniculatum*. Of the 35 floral visitors reported by Pandit and Choudhury (2001), 28 were not reported by Pandey and Pandey (2013b). On the other hand, of the 21 reported pollinators (including potential pollinators) of present work, 18 have not found by Pandit and Choudhury (2001) on east coast of India. Nevertheless, the floral visitors/pollinators of *A. corniculatum* reported in two mangrove forests viz. the Gulf of Kachchh (west coast of India) and Bhitarkanika (East coast of India) were found to be considerably different. Pollinator resource of *A. corniculatum* shows significant spatial and temporal variations within Marine National Park and Sanctuary, GOK, Gujarat (R. Pandey & C. N. Pandey, 2013b). Further, pollinator resource availability has been found to influence the overall reproductive success of mangroves and their further distribution (C. N. Pandey & R. Pandey, 2010a). Hence, *in situ* conservation of this species required comprehensive understanding of pollinator resources.

Table 12. Efficiency and availability of Pollinators at the three research sites

Group	Scientific Name/family	Efficiency	Relative Occurrence*					
			PP	PT	SN	PP	PT	SN
			Diurnal			Nocturnal		
Honey bees/bees	<i>Lasioglossum</i> sp.	Most efficient	A	A	C	R	MFV	R
	<i>Apis dorsata</i>	Most efficient	A	R	C	R	MFV	R
	<i>Apis florea</i>	Moderately efficient	A	A	C	R	MFV	R
	<i>Sphex umbrosus</i>	Most efficient	R	R	R	MFV	R	MFV
Bumble bees	<i>Scolia aureipennis</i>	Moderately efficient	R	R	R	MFV	R	MFV
	<i>Xylocopa aestuans</i>	Least efficient	R	R	R	MFV	R	MFV
Ants	<i>Crematogaster brunnea contemta</i>	Least efficient	R	R	R	A	C	C
Mosquitoes	Diptera -mosquito	Least efficient	MFV	R	R	R	C	C
	<i>Achaea janata</i>	Least efficient	MFV	MFV	MFV	R	C	R
	<i>Crocidolomia botalis</i>	Least efficient	MFV	MFV	MFV	R	C	R
Moths	<i>Utethesia latrice</i>	Least efficient	R	C	R	MFV	MFV	MFV
	<i>Helicoverpa armigera</i>	Least efficient	MFV	MFV	MFV	R	C	R
	<i>Spodoptera litura</i>	Least efficient	MFV	MFV	MFV	R	C	R
	Reed warber	Potential pollinators (probably most efficient)	MFV	R	R	R	R	R
Birds	<i>Nectarinia zeylonica</i>	Potential pollinators (probably most efficient)	MFV	R	R	R	R	R
	<i>Zosterops palpebrosus</i>	Potential pollinators (probably most efficient)	MFV	R	R	R	R	R
	<i>Anaphaeis aurota</i>	Potential pollinators	MFV	R	R	MFV	MFV	MFV
Butterflies	<i>Tirumala septemtrionis</i>	Potential pollinators	MFV	R	R	MFV	MFV	MFV
	<i>Vanessa cardui</i>	Potential pollinators	MFV	R	R	MFV	MFV	MFV
	Member of family- Lichniidae and Pieridae	Potential pollinators	MFV	R	R	MFV	MFV	MFV

Where *Source R. Pandey & C. N. Pandey (2013b), PT: Pirotan, PP: Patthapir, SN: Sanada, MFV: Minor Floral Visitor (less than 5%), A: Abundant, C: Common, R: Rare.

4.3 Reproductive Strategy

It is concluded that the floral biology of *A. corniculatum* strongly favors cross breeding. However, the asynchrony in flowering processes in inflorescences increases the possibility of geitonogamy. The pollination efficiency of pollinators and their availability also influence the reproductive biology of the species. For long term *in situ* conservation of this species, the pollinator resource needs to be conserved.

Acknowledgements

We are thankful to the Ministry of Environment and Forests, Government of India for sponsoring the project titled “Study of Pollination Biology and Reproductive Ecology of Major Mangrove Species of Gujarat” and extending full support to the project which made it possible to carry out the entire research. We are thankful to the entire staff at GEER Foundation, Gandhinagar for extending help from time to time. We would like to thank Dr. Harshad Salvi, Mrs. Urvi Joshi, Ms. Anjali Sharma, Mr. Sandeep Munjpara, Mr. Sandeep Patel, Mr. Virag Vyas, Mr. Nilesh Patel, for helping in field observations and to Mr. Sunil Panchal for photo documentation. We also thank, Pusa Institute, New Delhi, and Dr. Ramesh, Indian Forest Services, for identification of Pollinators.

References

- Almazol, A. E., & Cervancia, C. R. (2013). Floral biology and pollination of three mangrove species (*Aegiceras floridum* Roem. & Schults, *Schphiphora hydrophyllacea* Gaertn. F. and *Xylocarpus granatum* Koen) in Pagbilao Mangrove Forests, Quezon Province, Pilippines. *Journal of Nature Science*, 12(1), 39-47.
- Alonoso, A. T., & Herrera, C. M. (2008). Site-specific features affect pollination success of a gynodioecious understory shrub in a gender-specific mode. *Ecoscience*, 15, 358-365. <http://dx.doi.org/10.2980/15-3-3115>
- Aluri, R. J. (1990). Observations on the floral biology of certain mangroves. *Proceedings of the Indian National Science Academy, Part B. Biological Sciences*, 56(4), 367-374.
- Azuma, H., Toyota, M., Asakawa, Y., Takaso, T., & Tobe, H. (2002). Floral scent chemistry of mangrove plants, *Journal of Plant Research*, 115(1), 47-53. <http://dx.doi.org/10.1007/s102650200007>
- Banerjee, L. K., Shashtri, A. R. K., & Nayar, M. P. (1989). *Mangrove in India- Identification Manual*. Calcutta: Botanical Survey of India.
- Banerjee, L. K., Rao, T. A., Sastry, R. K., & Ghosh, D. (2002). *Diversity of coastal plant communities in India*. Kolkata: Botanical Survey of India.
- Clarke, P. J., & Myerscough, P. J. (1991). Floral biology and reproductive phenology of *Avicennia marina* in South-eastern Australia. *Australian Journal of Botany*, 39(3), 283-93. <http://dx.doi.org/10.1071/BT9910283>
- Clark, P. J. (1993). Dispersal of grey mangrove (*Avicennia marina*) propagules in southeastern Australia. *Aquatic Botany*, 45(2-3), 195-204. [http://dx.doi.org/10.1016/0304-3770\(93\)90021-N](http://dx.doi.org/10.1016/0304-3770(93)90021-N)
- Clarke, P. J. (1995). The population dynamics of the mangrove Shrub *Aegiceras corniculatum* (Myrsinaceae): fecundity, dispersal, establishment and population structure. *Proceedings of the Linnean Society of New South Wales*, 115, 35-44.
- Coupland, G. T., Paling, E. I., & McGuinness, K. A. (2005). Vegetative and reproductive phenologies of four mangrove species from northern Australia. *Australian Journal of Botany*, 53(2), 109-117. <http://dx.doi.org/10.1071/BT04066>
- Dafni, A. (1992). *Pollination Ecology: A Practical Approach*. New York: Oxford University Press.
- Dafni, A., & Maués, M. M. (1998). A rapid and simple method to determine stigma receptivity. *Sexual Plant Reproduction*, 2, 117-80.
- Darwin, C. (1888). *The different forms of flowers on plants of the same species. Facsimile edition, (1986)*. Chicago, IL, USA: University of Chicago Press.
- Davey, J. E. (1975). Notes on the Mechanism of Pollen Release in *Bruguiera gymnorhiza*. *Journal of South Africa Botany*, 41, 269-272.
- Debnath, H. S. (2004). *Mangroves of Andaman and Nicobar Islands: Taxonomy and Ecology (A community Profile)*. Bhisn Singh and Mahendra Pal Singh.
- Duck, N. C., Bunt, J. S., & Williams, W. T. (1984). Observations on the floral and vegetative phenologies of North-eastern Australian Mangroves. *Australian Journal of Botany*, 32, 87-99. <http://dx.doi.org/10.1071/BT9840087>
- Duck, N. C. (2006). *Australia's Mangroves- the authoritative guide to Australia's mangrove plants*. University of Queensland, Brisbane.
- Elliot, N. B., Edward, D. C., & Godfrey, P. J. (1996). *Proceedings of the sixth symposium on the natural history of the Bahamas*. In A. S. Linda, M. M. Godfrey, D. R. Suchy & N. G. Suchy (Eds.), Pub. Bahamian Field Station, Bahamas.
- Ellison, A. M. (2008). Managing mangroves with benthic biodiversity in mind: moving beyond roving banditry. *Journal of Sea Research*, 59, 2-15. <http://dx.doi.org/10.1016/j.seares.2007.05.003>
- Ge, X. J., & Sun, M. (1999). Reproductive biology and genetic diversity of a crypto-viviparous mangrove *Aegiceras corniculatum* (Myrsinaceae) using allozyme and intersimple sequence repeat (ISSR) analysis. *Molecular Ecology*, 8, 2061-2069. <http://dx.doi.org/10.1046/j.1365-294x.1999.00821.x>
- GEER. (2000). *Mangroves of Gujarat*, Gujarat Ecological Education and Research (GEER) Foundation, Gandhinagar.
- Geng, Q., Lian, C., Goto, S., Tao, J., Kimura, M., Islam, M. S., & Hogetsu, T. (2008). Mating system, pollen and

- propagule dispersal and spatial genetic structure in a high-density population of the mangrove tree *Kandelia candel*. *Molecular Ecology*, 17, 4724-4739. <http://dx.doi.org/10.1111/j.1365-294X.2008.03948.x>
- Ghosh, A., Gupta, S., Maity, S., & Das, S. (2008). Study of floral morphology of some Indian mangroves in relation to pollination. *Research Journal of Botany*, 3(1), 9-16. <http://dx.doi.org/10.3923/rjb.2008.9.16>
- Ghosh, A., & Chakraborti, P. (2011). Evaluation of some mangrove species on the nature of their reproduction along the coastal belt of the Indian Sunderbans. *Journal of Threatened Taxa*, 4(3), 2427-2435. <http://dx.doi.org/10.11609/JoTT.o2416.2427-35>
- Goethe, J. W. V. (1790). *Versuch, die Metamorphose der Pflanzen zu erklären*, C.W. Ettinger, Gotha. Reprint (D. Kuhn, ed.), Verlag Chemie, Weinheim, 1984.
- Harder, L. D., & Barrett, S. C. H. (1996). Pollen dispersal and mating patterns in animal-pollinated plants. In D. G. Lloyd, S. C. H. Barrett (Eds.), *Floral biology: studies on floral evolution in animal-pollinated plants*. (pp. 140-190). New York, NY, USA: Chapman & Hall.
- Henschel, A. W. (1820). *Von der Sexualität der Pflanzen.*, W.G. Korn, Breslau.
- Homer, L. E. (2009). Population structure and distance of gene flow in *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae) on a local/ regional scale in the Northern Rivers of New South Wales, Australia', *PhD thesis, Southern Cross University, Lismore, NSW*.
- Johansen, D. A. (1940). *Plant Microtechnique*. New York: McGraw-Hill Book Company.
- Juncosa, A. M., & Tomlinson, P. G. (1987). Floral development in mangrove Rhizophoraceae. *American Journal of Botany*, 74(8), 1263-1279. <http://dx.doi.org/10.2307/2444162>
- Kado, T., Fujimoto, A., Le, H. G., Tuan, M., Phan, N. H., Harada, K., & Tachida, H. (2004). Genetic structure of natural populations of three mangrove species, *Avicennia marina*, *Kandelia candel* and *Lumnitzera racemosa*, in Vietnam revealed by maturase sequences of plastid DNA. *Plant Species Biology*, 19(2), 91-99. <http://dx.doi.org/10.1111/j.1442-1984.2004.00107.x>
- Kamruzzaman, Md., Sharma, S., & Hagihara, A. (2013). Vegetative and reproductive phenology of the mangrove *Kandelia obovata*. *Plant Species Biology*, 28, 118-129. <http://dx.doi.org/10.1111/j.1442-1984.2012.00367.x>
- Kathiresan, K., & Bingham, B. L. (2001). Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology*, 40, 181-251. [http://dx.doi.org/10.1016/S0065-2881\(01\)40003-4](http://dx.doi.org/10.1016/S0065-2881(01)40003-4)
- Kölreuter, G. J. (1761-1766). *Vorläufige Nachricht von einigen, das Geschlecht der Pflanzen betreffenden Versuchen*.
- Lakshmi, M., Rajalakshmi, S., Parani, M., Anuratha, C. S. I., & Parida, A. (1997). Molecular phylogeny of mangroves I. Use of molecular markers in assessing the intraspecific genetic variability in the mangrove species *Acanthus ilicifolius* Linn. (Acanthaceae). *Theory of Applied Genetics*, 94, 1121-1127. <http://dx.doi.org/10.1007/s001220050525>
- Lakshmi, M., Parani, M., & Parida, A. (2002). Molecular phylogeny of mangroves IX, molecular marker assisted intra-specific variation and species relationships in the Indian mangrove tribe Rhizophoreae, *Aquatic Botany*, 74, 201-217. [http://dx.doi.org/10.1016/S0304-3770\(02\)00105-5](http://dx.doi.org/10.1016/S0304-3770(02)00105-5)
- Landry, C. L., & Rathcke, B. J. (2007). Do inbreeding and relative male fitness explain the maintenance of androdioecy in white mangrove, *Laguncularia racemosa* (Combretaceae). *New Phytologist*, 176, 891-901. <http://dx.doi.org/10.1111/j.1469-8137.2007.02228.x>
- Lieu, N. T. H., & Hong, P. N. (2004). Some development stages of the reproductive organs of *Aegiceras corniculatum* (L.) Blanco naturally growing in the coastal area of Northern Vietnam, In P. N. Hong (Ed.), *Mangrove ecosystem in the red river coastal zone, biodiversity, ecology, socio-economics, management and education* (pp.175-182). Agricultural Publishing House.
- Maguire, T. L., Saenger, P., Baverstock, P., & Henry, R. (2000). Microsatellite analysis of genetic structure in the mangrove species *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae). *Molecular Ecology*, 9, 1853-1862. <http://dx.doi.org/10.1046/j.1365-294x.2000.01089.x>
- McGuinness, K. A. (1997). Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. *Oecologia (Berlin)*, 109, 80-87. <http://dx.doi.org/10.1007/s004420050061>
- Melville, F., & Burchett, M. (2002). Genetic variation in *Avicennia marina* in three estuaries of Sydney, (Australia) and implications for rehabilitation and management. *Marine Pollution Bulletin*, 44(6), 469-479.

- [http://dx.doi.org/10.1016/S0025-326X\(01\)00259-4](http://dx.doi.org/10.1016/S0025-326X(01)00259-4)
- Meyer, D. E. (1953). Biographisches und Bibliographisches über Christian Konrad Sprengel. *Willdenowia; Mitt. Bot. Gart. Mus. Berlin-Dahlem*, 1, 118-125.
- Morrissey, D. J., Swales, A., Dittmann, S., Morrison, M. A., Lovelock, C. E., & Neard, C. M. (2010). Ecology and management of temperate mangroves. *Oceanography and Marine Biology: An Annual Review*, 48, 43-160. <http://dx.doi.org/10.1201/EBK1439821169-c2>
- Nadia, T., De L., Menezes, De N. L., & Machado, I. C. (2013). Floral traits and reproduction of *Avicennia schaueriana* Moldenke (Acanthaceae): a generalist pollination system in the Lamiales. *Plant Species Biology*, 28, 70-80. <http://dx.doi.org/10.1111/j.1442-1984.2011.00361.x>
- Nagrajan, P., Pandiarajan, C., Krishnmoorthy, M., & Sophia, P. (2008). Reproductive fitness and success in mangroves: implication on conservation in *Proceedings of Taal 2007, The 12th World Lake conference*. In (Eds.) M. Sengupta & R. Dalwani, (pp. 29-33).
- Naskar, K. R. (2004). *Manual of Indian Mangroves*. Daya Publishing House, Delhi.
- Noske, R. A. (1993). *Bruguiera hainesii*: another bird-pollinated mangrove? *Biotropica*, 25, 481-483. <http://dx.doi.org/10.2307/2388873>
- Odum, W. E., McIvor, C. C., & Smith, III, T. J. (1982). *The ecology of the mangroves of south Florida: a contry profile*. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-81/24.
- Pandey, C. N., & Pandey, R. (2009). *Floristic diversity and natural recruitment of mangroves in selected habitats of South Gujarat*, GEER Foundation, Gandhinagar.
- Pandey, C. N., & Pandey, R. (2010a). *Study of pollination biology and reproductive ecology of three major mangrove species of Gujarat*, GEER Foundation, Gandhinagar.
- Pandey, R., Pandey, C. N., & Jain, B. K. (2010b) Reproductive phenology of *Rhizophora mucronata* Lamk. (Rhizophoraceae) in Gulf of Kachchh, Gujarat, India. *Phytomorphology*, 60 (3&4), 91-100.
- Pandey, R., & Pandey, C. N. (2013a). Reproductive phenology of *Aegiceras corniculatum* (L) Blanco- a mangrove species in the Gulf of Kachchh, Gujarat, India, *International Journal of Botany and Research*, 3, 19-28.
- Pandey, R., & Pandey, C. N. (2013b). Spatial and temporal variations in floral visitors of a mangrove species - *Aegiceras corniculatum* (L.) Blanco – in the Marine National Park, Gujarat, India. *International Journal of Botany and Research*, 3, 35-42.
- Pandey, R., & Pandey, C. N. (2013c). Floral biology and pollination ecology of *Rhizophora mucronata* Lamk. in Gulf of Kachchh, Gujarat, India. *International Journal of Botany and Research* (in press).
- Pandit, S., & Choudhury, B. C. (2001). Factors affecting pollinator visitation and reproductive success in *Sonneratia alba* and *Aegiceras corniculatum* in a mangrove forest in India. *Journal of Tropical Ecoogy*, 17, 431-447. <http://dx.doi.org/10.1017/S0266467401001584>
- Rajgopalan, M. S. (1987). Mangroves as component of coastal ecosystem of Andaman's. In: *Proc. Symp. Manag. Coastal Ecosystem and Oceanic resources of Andamans*. Andaman Sci. Asso. Port Blair. 1-7.
- Richards, A. J. (1997). *Plant breeding systems*. New York, NY, USA: Chapman & Hall.
- Sánchez-Núñez, D. A., & Mancera-Pineda, J. E. (2011). Flowering patterns in three neotropical mangrove species: Evidence from a Caribbean island. *Aquatic Botany*, 94(4), 177-18. <http://dx.doi.org/10.1016/j.aquabot.2011.02.005>
- Seetharaman, K., & Kathiresan, K. (2011). Reproductive biology of a natural mangrove hybrid *Rhizophora annamalayana* and its parent species (*R. apiculata* and *R. mucronata*) (Rhizophoraceae), *Botanica Marina*, 54(6), 583-589. <http://dx.doi.org/10.1515/BOT.2011.062>
- Solomon Raju, A. J., Jonathan, K. H., & Vijaya Lakshmi, A. (2006). Pollination biology of *Ceriops decandra* (Griff.) Ding Hou (Rhizophoraceae)- an important true viviparous mangrove species. *Current Science*, 91(9), 1235-1238.
- Solomon Raju, A. J., & Karyamserry, H. J. (2008). Reproductive ecology of mangrove trees *Ceriops decandra* (Griff.) Ding Hou and *Ceriops tagal* (Perr.) C. B. Robinson (Rhizophoraceae). *Acta Botanica Croatica*, 67(2), 201-208.

- Solomon Raju, A. J., Rao, P. V., Kumar, S. R., & Mohan, S. R. (2012). Pollination biology of the crypto-viviparous *Avicennia* species (Avicenniaceae). *Journal of Threatened Taxa*, 4(15), 3377-3389. <http://dx.doi.org/10.11609/JoTT.o2919.3377-89>
- Sprengel, C. K. (1793). *Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen I*. Vieweg sen., Berlin Reprint by J. Cramer, H. K. Swann, Lehre, Weldon & Wesley, Codicote, New York. <http://dx.doi.org/10.5962/bhl.title.50179>
- Steinke, T. D. (1986). A preliminary study of buoyancy behaviour in *Avicennia marina* propagules. *South African Journal of Botany*, 52, 559-565.
- Steinke, T. D. (1988). Vegetative and floral phenology of three mangroves in Mgeni Estuary. *South African Journal of Botany*, 54, 97-102.
- Stocken, T., Van der, De Ryck, D. J. R., Balke, T., Bouma, T. J., Dahdouh-Guebas, F., & Koedam, N. (2013). The role of wind in hydrochorous mangrove propagule dispersal. *Biogeosciences Discuss.*, 10, 895-925. <http://dx.doi.org/10.5194/bgd-10-895-2013>
- Sun, M., Wong, K. C., & Lee, J. S. Y. (1998). Reproductive biology and population genetic structure of *Kandelia candel* (Rhizophoraceae), a viviparous mangrove species. *American Journal of Botany*, 85, 1631-1637. <http://dx.doi.org/10.2307/2446492>
- Tomlinson, P. B. (1986). *The botany of mangroves*. New York: Cambridge University Press.
- Tomlinson, P. B., Primack, R. B., & Bunt, J. S. (1979). Preliminary observations on the floral biology in mangrove Rhizophoraceae. *Biotropica*, 11, 256-277. <http://dx.doi.org/10.2307/2387918>
- Vogel, S. (1996). Christian Konrad Sprengel's theory of the flower: the cradle of flower ecology. In G. L. David & C. H. Spencer (Eds.), *Floral biology: studies on floral evolution in animal pollinated plants* (pp. 44-62). Florence: International Thomson Publishing.
- Willdenow, C. L. (1802). *Grundriss der Kräuterkunde, zu Vorlesungen entworfen* (3rd ed.) Haude & Spener, Berlin.
- Willson, M. F. (1983). *Plant reproductive ecology*. New York, NY, USA: John Wiley and Sons. <http://dx.doi.org/10.1007/BF00047100>
- Wyatt, R. (1983). Pollinator-plant interactions and the evolution of breeding systems. In L. Real (Ed.) *Pollination biology* (pp. 51-95). Orlando, FL, USA: Academic Press.
- Yamashiro, M. (1961). Ecological study on *Kandelia candel* (L.) Druce, with special reference to the structure and falling of the seedling. *Hikobia*, 2, 209-214.

Copyrights

Copyright for this article is retained by the author(s), with first publication rights granted to the journal.

This is an open-access article distributed under the terms and conditions of the Creative Commons Attribution license (<http://creativecommons.org/licenses/by/3.0/>).