

# Pollination ecology of the coastal pantropical hermaphroditic shrub *Scaevola taccada* (Goodeniaceae)

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**Abstract.** *Scaevola taccada* is a coastal evergreen bushy shrub. It blooms throughout the year but intense flowering occurs only during the wet season. The flowers are fan-shaped, bisexual, protandrous, nectariferous, self-compatible and display a secondary pollen presentation mechanism, which principally facilitates cross-pollination while keeping the option open for self-pollination. Flower foragers include bees, wasps, ants, and moths but certain bees and all wasps are principal pollinators, while moths are minor pollinators. Certain other bees and ants act as mere nectar robbers but they appear to compel pollinators to make multiple visits to the flowers thus promoting the pollination rate. The pollinator bees collect only nectar and effect nototribic pollination, which facilitates pollen deposition precisely on their back for effective transfer to other flowers and precludes access to pollen for insect grooming by their legs. Fruit set occurs both in self- and cross-pollination but a significant percentage of fruit abortion occurs in self-pollinated flowers, indicating an inherent regulatory mechanism, which terminates the genetically inferior fruits. Fruits with pulpy exocarp, corky mesocarp and stone-hard endocarp are buoyant and hydrochorous. Seeds germinate and produce new plants on sandy beaches. The plant also propagates by vegetative means through rooting from aerial stems that touch the ground, and also by stem cuttings. The plant is important for sand erosion control, beach stabilization and landscaping through plantation activity. Therefore, it is a promising species for the restoration of coastal vegetation.

**Key words:** *Scaevola taccada*, hermaphroditism, protandry, secondary pollen presentation mechanism, facultative xenogamy, entomophily, nototriby, hydrochory.

## Introduction

Goodeniaceae consists of 12 genera with 430 species distributed mostly in Australia (Stevens 2012). *Scaevola* (Gaertn.) Roxb. is one of the genera in this family, composed of approximately 130 species, most of which are native to Australia, while some 40 species are distributed outside Australia. The genus name comes from the Greek word *scaevus*, which means left-handed, describing the floral characteristic. The flowers are irregular, split in half and, hence, are commonly called "half-flowers" (Wagner & al. 1990;

Stone & Pratt 1994). This state of flowers is attributed to a love story in which a woman tears the flower of *Scaevola* in half after a quarrel with her lover. Then the gods angered and turned all flowers into half flowers and the two lovers remained separated, while the man was destined to search in vain for another whole flower (Hammer 1998). Free anthers and 1-2-seeded indehiscent drupe are important distinguishing features of *Scaevola* from other members of the Goodeniaceae family (Carolin & al. 1992). *Scaevola* flowers are fan-shaped, bisexual, zygomorphic, nectariferous, protandrous, and display secondary pollen presentation

adapted for out-crossing (Clarke & Lee 1987; Howell & al. 1993; Ladd 1994). In this genus, two species, *S. taccada* and *S. plumieri* are widespread strand species, the former is distributed throughout the Pacific and Indian Ocean, while the latter is distributed in the tropical Americas and Africa (Howarth & al. 2003). Their wide distribution in part is attributed to their ability to disperse through birds and ocean floating (Lesko & Walker 1969). The remaining species of this genus are narrower endemics, often occurring well inland as forest trees or shrubs (Howarth et al. 2003). In North America, *S. taccada* has become invasive and affects the sexual reproduction and population build up by *S. plumieri* (Elmore 2008). Emura & al. (2014) reported that *S. taccada* distributed on Okinawan Islands of Japan display dimorphism in the internal structure of the fruits. These authors classified them as C-morph and NC-morph types which are produced on different plants. The endocarp consists of cork and pulp in the C-morph and only of pulp in the NC-morph. The frugivorous birds *Monticola solitarius* and *Hypsipetes amaurotis* feed on the fruit pulp of both morph types but they are important only for NC-morph fruits for their dispersal, because they cannot float in ocean water, while the C-morph fruits principally disperse in ocean water because they have floating ability.

Howell (1995) reported that *S. taccada* is strictly self-incompatible and exhibits secondary pollen presentation. Liao (2008) reported that *S. taccada* is xenogamous but has the potential for self-pollination. It is visited and pollinated mainly by bees, particularly *Apis mellifera*, on the South Pacific Island, Mo'orea. Furthermore, he have also noted that wind speed has a role on the visitation rate of bees to the flowers. On the Hawaii Island, *S. taccada* is reported to be mostly visited by bees (Gillett 1966; van Balgooy & Carolin 1975). Subsequently, Elmore (2008) noted that *S. taccada* is pollinated mostly by non-native bees and occasionally by native bees on the same island. These authors did not provide details on the foraging behavior resulting in pollination by different bee species. In India, there are absolutely no studies on *S. taccada*, despite its importance as a constituent taxon of coastal flora. This plant is used in traditional medicine in the places of its occurrence. Fruit juice is used internally to induce menstruation (Khare 2007) and externally to treat sores and infected eyes (Barr & al. 1993; Khare 2007). A combination of juice from ripe fruit

and stem is used as a remedy for bites and stings (Barr et al. 1993). Leaf decoction and seed flesh are used as contraceptives (Cambie & Brewis 1997). Root decoction is used to treat stomach ache, urinary problems and pain in the alimentary tract, while stem decoction is used to cure boils, skin rashes and sores (Cribbs & Cribbs 1981). The plant is also used in the treatment of cancer and as bush tonic in traditional aboriginal medicine in Australia (Longmore & Kerr 1997). In India, the distribution of *S. taccada* in the coastal areas is not documented systematically. Rao & al. (1983) documented that *S. taccada* grows as a large bushy shrub along the back-shore strand and is widely spread all along the West Coast. Further, it occurs only at Rambille coastal area in Andhra Pradesh. Sudhakar (1980) noted that *S. taccada* occurs along Visakhapatnam coast in Andhra Pradesh. Recent surveys along the entire stretch of Visakhapatnam coast carried out by us indicated that *S. taccada* has completely disappeared due to some major land use changes along the coast. However, a large patch of this plant has been found near Chepala Kancheru village located on the bank of Bay of Bengal in Bhoghapuram Mandal in Vizianagaram district of Andhra Pradesh. The present study is aimed at investigating the floral morphology and biology, sexual system, pollination mechanism, pollinators, and fruiting ecology of *S. taccada*, because the information on these aspects is essential for taking measures for its protection and expansion of its distribution along the coast.

## Material and methods

Wild population of *Scaevola taccada* spreads over 20 meters along the shoreline of the Bay of Bengal near Chepala Kancheru village (Lat. 17.9700346°N and Long. 83.5439957°E) in Bhoghapuram Mandal, Vizianagaram district of Andhra Pradesh, India. It was selected for study during April 2017 – January 2019. In the same area, about 200 m long plantation from stem cuttings of this species developed by the area manager was also used for recording observations on its growth rate and use as initial species for the development of coastal vegetation. Observations of the organization of inflorescences, spatial positioning of flowers and their position on the plant were carried out, since these features are regarded as important for foraging and pollination by flower visitors. The flower

longevity was recorded by marking twenty just open flowers and following them until fall off. Anthesis was initially recorded by observing ten marked mature buds in the field. Later, the observations were repeated five times on different days, each day observing ten marked mature buds, in order to provide accurate anthesis schedule. The same marked mature buds were followed for recording the time of anther dehiscence. The presentation pattern of pollen was also investigated by recording how anthers dehisced and confirmed by scrutinizing the anthers under a 10× hand lens. The details of flower morphology such as flower sex, shape, size, color, odor, sepals, petals, stamens, and ovary were described.

Twenty-five mature but undehiscent anthers were collected from five randomly chosen plants and placed in a Petri dish. Subsequently, each anther was taken out and placed on a clean microscope slide (75 × 25 mm) and dabbed with a needle in a drop of lactophenol-aniline-blue. The anther tissue was then observed under the microscope for pollen, and if pollen grains were not found, the tissue was removed from the slide. The pollen mass was drawn into a band, and the total number of pollen grains was counted under a compound microscope (40× objective, 10× eyepiece). This procedure was followed for counting the number of pollen grains in each collected anther. On the basis of these counts the mean number of pollen produced per anther was determined. The characteristics of pollen grains were also recorded. The stigma receptivity was checked by H<sub>2</sub>O<sub>2</sub> test, as given in Dafni & al. (2005).

The presence of nectar was determined by observing twenty-five mature buds and open flowers collected at random from ten plants. Individual volumes of nectar were recorded for twenty flowers and then the average volume of nectar per flower was determined and recorded in µl. The flowers used for this purpose were bagged at mature bud stage, opened after anthesis and nectar squeezed into micropipette to measure its volume. Nectar sugar concentration was also simultaneously determined by a Hand Sugar Refractometer (Erma, Japan).

Fifty flowers each from ten randomly selected plants were used for each mode of breeding system. The stigmas were pollinated manually with the pollen of the same flower by a brush; they were bagged for fruit set through manipulated autogamy. The flowers were fine-mesh bagged without hand pollination for

fruit set through spontaneous autogamy. The emasculated flowers were hand-pollinated with the pollen of a different flower on the same plant; they were bagged and watched for fruit set through geitonogamy. The emasculated flowers were pollinated with the pollen of a different individual plant and bagged for fruit set through xenogamy. All these modes of pollination were followed for one month in order to calculate the percentage of fruit set in each mode. Twenty inflorescences consisting of one hundred and twenty-five flowers were tagged on twenty plants prior to anthesis and watched for fruit set rate in open pollinations. Fruit maturation period, fruit dehiscence, seed dispersal and establishment were observed in detail.

The insects visiting the flowers were watched closely for ten hours a day in the course of fifteen days in different weeks during peak flowering season. The hourly foraging visits of each species were recorded on ten different days, for the purpose of which thirty inflorescences were selected. The data obtained was used to calculate the percentage of foraging visits made by each species per day, in order to understand the relative importance of each species. Along with this, they were observed for their foraging behavior such as mode of approach, landing, probing, the type of forage they collect, contact with essential organs to result in pollination, and inter-plant foraging activity. The pollinator insect species were captured on the flowers during 09:00–11:00 time period on five different days for pollen analysis in the laboratory. For each species, 10 specimens were taken and each specimen was washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present. From pollen counts, the average number of pollen grains carried by each species was calculated to have the pollen carryover efficiency of different insect species.

## Results

### Flowering phenology and flower morphology.

The plant is a large bushy evergreen shrub growing close to the sea and exposed to the salt spray on sandy and pebbly soils (Fig. 1a-c). The branches root when they contact the ground forming a rhizome, then new shoots grow up and thus the plant spreads easily, colonizing the area by vegetative mode (Fig. 1d).



**Fig. 1.** *Scaevola taccada*: **a.** & **b.** Habitat with wild patch, along with plantation from stem cuttings, **c.** Shrubby habit, **d.** New shoot formation from creeping rhizome.

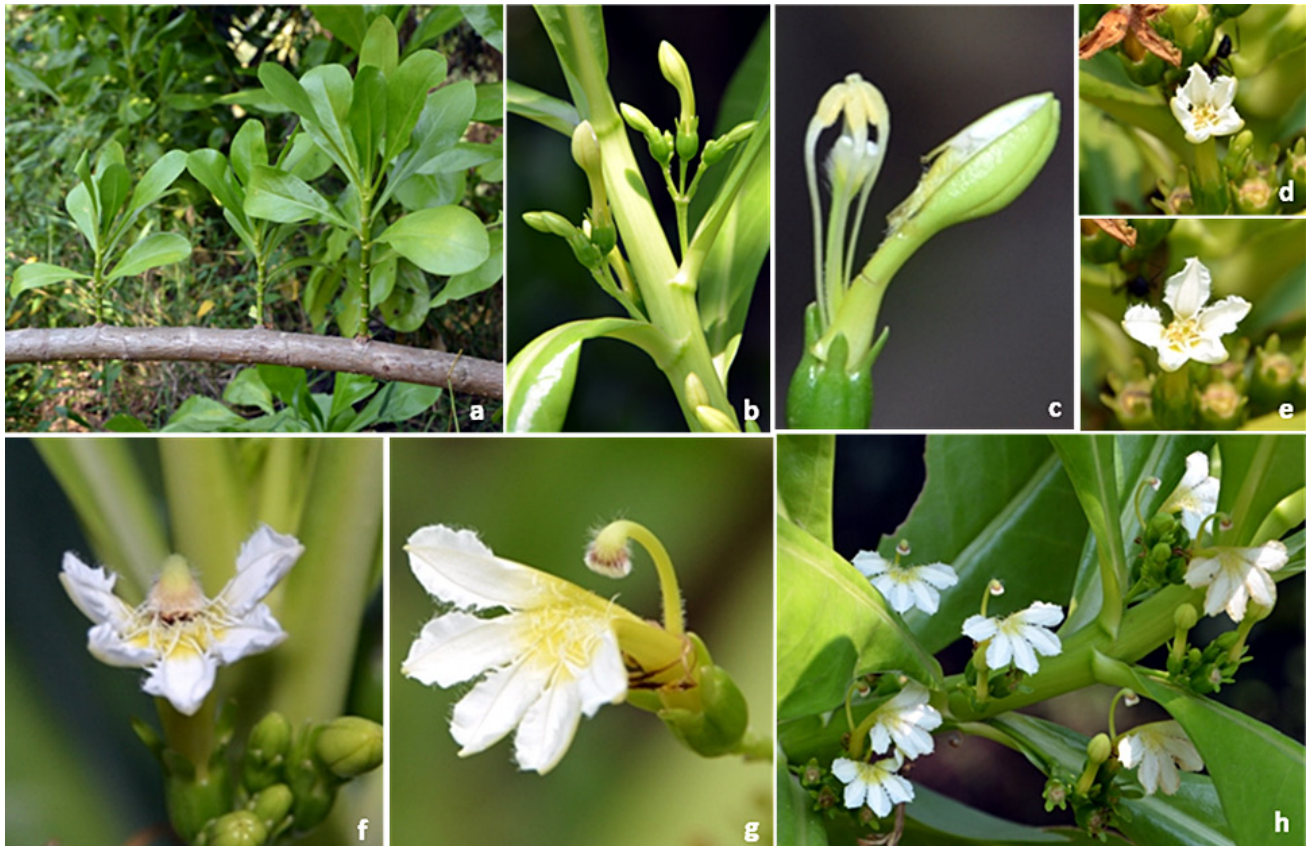
The leaves are succulent, glabrous, yellowish-green, oblanceolate, with rolled margins and rounded tips, and crowded at the stem tips (Fig. 2a). The flowering occurs throughout the year, but is profuse during the rainy season from June to October. The flowers are aggregated in axillary cymes and remain partly covered by leaves (Fig. 2b, h). Individual cymes produce  $6.54 \pm 1.84$  flowers, which open over a period of 3–4 days.

The flowers are pedicellate, milky-white, fragrant, fan-shaped,  $17.97 \pm 0.07$  mm long,  $20.12 \pm 0.05$  mm wide, bisexual and zygomorphic. The calyx is well developed, green, and gamosepalous with five lobes. The corolla has five irregularly-shaped white petals produced on one side of the flower making it appear as half-flower; it is tubular at base and measuring  $10.18 \pm 0.09$  mm in length, hairy adaxially and at the rim of the corolla throat. The stamens arise from the base of the corolla tube; they are five, free, arranged opposite to sepals and tipped with basifixed, introrse yellow anthers. The ovary is bicarpellary, bilocular syncarpous, with one ovule on axile placentation in each locule. It is monostylous, with its apical part extended as an outgrowth called

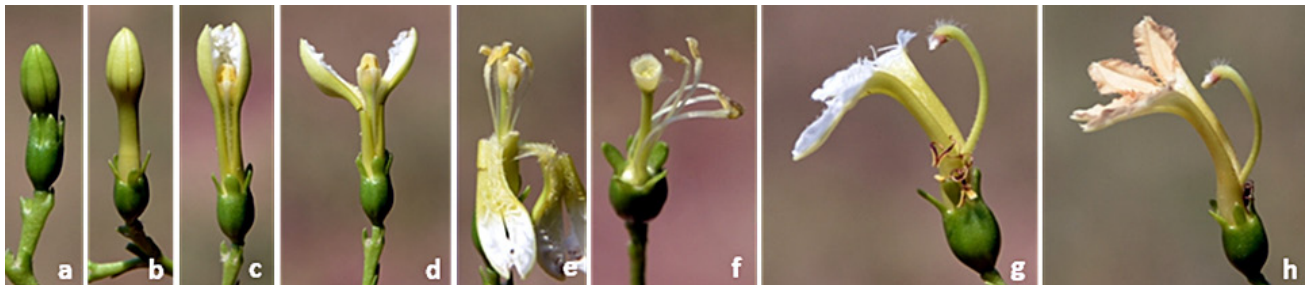
"indusium" or "stylar cup" and surrounding the stigma initially. Subsequently, the stigma grows out of the stylar cup and appears as a 2-lobed structure. The style with its apical cup functions as an upper lip and faces the zygomorphic corolla forming the lower lip.

### Floral biology

Mature buds open during 07:00–10:00 hrs. Individual flowers open gradually over a period of about two hours (Figs 2d-g; 3a-c). Nectar is secreted in small quantities and amounts to  $2.7 \pm 0.32$   $\mu$ l per flower; the sugar concentration is  $16.85 \pm 0.83$  %. The anthers dehisce all at once during mature bud stage. The pollen output is  $1382.9 \pm 125.07$  per anther and  $6914.5 \pm 625.36$  per flower. The pollen-ovule ratio is 3457.25:1. The pollen grains are light-yellow, tricolporate, sub-oblato to prolate, with some scattered spinules,  $37.35 \pm 4.37$   $\mu$ m in size; the sexine is conspicuously thicker than nexine throughout, except in the area of the colpi. The stigma is receptive after flower opening and remains receptive until the evening of the 2<sup>nd</sup> day. Then, the flowers turn brown, which is prominent on the



**Fig. 2.** *Scaevola taccada*: **a.** Emergence of leaf branches from the main shoot, **b.** Axillary inflorescences with immature and maturing buds, **c.** Stigma over-arched by stamens during mature bud stage, **d-g.** Stages in the anthesis, **h.** Flowers from different axillary inflorescences.



**Fig. 3.** *Scaevola taccada*: **a.** Initial bud, **b.** Mature bud, **c.** Initiation of anthesis, **d.** Stigma over-arched by stamens during mature bud stage, **e. & f.** Anther dehiscence and deposition of pollen in stigma cup, **g.** Fresh flower with stamens curling backwards and placement at the base of the corolla tube, **h.** 3-day old flower.

morning of the 3<sup>rd</sup> day (Fig. 3h), and subsequently the corolla and stamens fall off mostly on the 4<sup>th</sup> day in pollinated and unpollinated flowers. The calyx is persistent and turns into fruiting calyx in fertilized flowers, while the calyx and pistil wither and remain intact in unpollinated flowers.

### Pollination mechanism

In mature bud stage, the style and stigma are situated below the anthers (Fig. 2c, 3d). The style has a terminal stylar cup, which encloses the stigma inside. The

staminal filaments grow quickly, elevating the anthers above the stylar cup. As the anthers are introrse and dehisce simultaneously, the pollen mass slides into the stylar cup, while the style elongates by rapid growth (Fig. 3e-f). After pollen discharge, the anthers and the filaments wither and curl downwards to the corolla base (Fig. 3g). The stylar cup loaded with its own pollen closes and style bends downwards as the flower opens. When the flower opens, the stylar cup faces the fan-shaped corolla. Long stiff hairs occur around the border of the stylar cup, covering densely the adaxial

side and sparsely the abaxial side. These hairs cover the cup outside and the upper part of the style. As the stigma continues to grow, it gradually protrudes from the stylar cup pushing the pollen out, which is then removed portion by portion by pollinators nototribically, and ultimately the stigma is fully exposed and receptive for pollen. The relocation of pollen from the anthers to the stylar cup is an indication of the function of secondary pollen presentation and protrusion of the stigma through the stylar cup makes the pollen available for pollination. This mode of pollen presentation also facilitates the adherence of pollen to the stigma emerging from the stylar cup, thus providing a chance for the occurrence of autogamy. The pollination mechanism functional in this plant indicates that protandry promotes out-crossing, while keeping the self-pollinating option, if pollination does not occur.

### Breeding system

Hand-pollination tests showed that the plant produces fruit through self- and cross-pollination. Fruit set rate varied from 12–30 % in un-manipulated and

manipulated autogamy, 58 % in geitonogamy, 82 % in xenogamy, and 87 % in open pollination. The results indicated that fruit set is the highest in xenogamy and lowest in unmanipulated autogamy among the hand-pollination tests. Fruit set evidenced in open pollination is regarded as product of auto-, geitono- and xenogamy (Table 1). However, within one week of fruit initiation, a major percentage of fruit abortion was recorded in autogamy and geitonogamy: 83–90 % in unmanipulated and manipulated autogamy, and 71 % in geitonogamy. Fruit abortion was absent in xenogamy. Fruit abortion was 56 % in open pollinations and this high percentage of abortion was regarded as resulting from selective termination of growing fruits, mostly from self-pollination.

### Flower-visitors and pollination

For daytime nectar collection in the period 08:00–18:00 hrs, with peak foraging activity during 09:00–11:00 hrs, the flowers were visited by: bees, such as *Apis dorsata* (Fig. 4a-c), *A. cerana* (Fig. 4d,e), *A. florea*, *Anthophora bicincta* (Fig. 4h), *Lasioglossum* sp.



**Fig. 4.** *Scaevola taccada*: Foragers: **a.** *Apis dorsata* on day 1 flower, **b.** *Apis dorsata* on day 2 flower, **c.** *Apis dorsata* on day 3 flower, **d. & e.** *Apis cerana* on day 1 flowers, **f.** *Megachile* sp. on day 1 flower, **g.** *Megachile* sp. on day 1 flower, **h.** *Anthophora cingulata* on day 3 flower, **i.** *Lasioglossum* sp. on day 1 flower, **j.** *Vespa bicincta* on day 3 flower, **k.** *Campsomeris annulata* on day 1 flower, **l.** *Campsomeris annulata* on day 3 flower, **m.** *Scolia* sp. on day 1 flower, **n.** *Scolia* sp. on day 3 flower, **o.** Hesperiid butterfly, *Suastus gremius* on day 3 flower.

(Fig. 4i), and *Megachile* spp. (Fig. 4f,g); wasps, such as *Vespa bicincta* (Fig. 4j), *Scolia* sp. (Fig. 4m,n) and *Campsomeris annulata* (Fig. 4k,l); and the Hesperidae moth, *Suastus gremius* (Fig. 4o); . The Sphingidae hawk moth, *Deilephila* sp., foraged for two hours in the evening, at 17:00–18:00 hrs (Table 2; Fig. 6). Of all these flower-visitors, bees accounted for 70 %, wasps for 23 % and moths for 7 % of all foraging visits (Fig. 7). The moths were occasional foragers, while all other foragers were regular and consistent, especially during

peak flowering season. All insect species approached the flowers in upright position, used the corolla fan as a landing platform and inserted their mouth parts and head into the corolla base for nectar collection. In this posture, *A. florea*, *A. bicincta*, *Lasioglossum* sp., and *Megachile* spp. never had contact with the stylar cup, while probing the flower for nectar. *Megachile* spp., after collecting nectar, occasionally attempted to collect pollen from the stylar cup by standing almost erect on the corolla-fan but this pollen collection activity was

**Table 2.** List of insect foragers recorded on *Scaevola taccada*.

| Order       | Family        | Genus               | Species            | Common name        | Forage sought  |
|-------------|---------------|---------------------|--------------------|--------------------|----------------|
| Hymenoptera | Apidae        | <i>Apis</i>         | <i>dorsata</i> F.  | Rock Bee           | Nectar         |
|             |               | <i>Apis</i>         | <i>cerana</i> F.   | Indian Honey Bee   | Nectar         |
|             |               | <i>Apis</i>         | <i>florea</i> F.   | Dwarf Honey Bee    | Nectar         |
|             | Anthophoridae | <i>Anthophora</i>   | <i>bicincta</i> L. | Blue Banded Bee    | Nectar         |
|             | Halictidae    | <i>Lasioglossum</i> | sp.                | Sweat Bee          | Nectar         |
|             | Megachilidae  | <i>Megachile</i>    | spp.               | Leaf Cutter Bee    | Nectar, Pollen |
|             | Vespidae      | <i>Vespa</i>        | <i>bicincta</i> F. | Yellow Banded Wasp | Nectar         |
|             | Scoliidae     | <i>Scolia</i>       | sp.                | Blue Winged Wasp   | Nectar         |
|             |               | <i>Campsomeris</i>  | <i>annulata</i> F. | Flower Wasp        | Nectar         |
| Lepidoptera | Hesperiidae   | <i>Suastus</i>      | <i>gremius</i> F.  | Indian Palm Bob    | Nectar         |
|             | Sphingidae    | <i>Deilephila</i>   | sp.                | Elephant Hawk Moth | Nectar         |



**Fig. 5.** *Scaevola taccada*: **a.** C-fruit morph with pulpy epicarp, corky mesocarp and stone-hard endocarp, **b.** Production of C-fruit morph and NC-fruit morph (thin pulpy epicarp and stone-hard endocarp) on the same plant, **c-f.** Different stages of shoot and leaf production from stem cuttings.

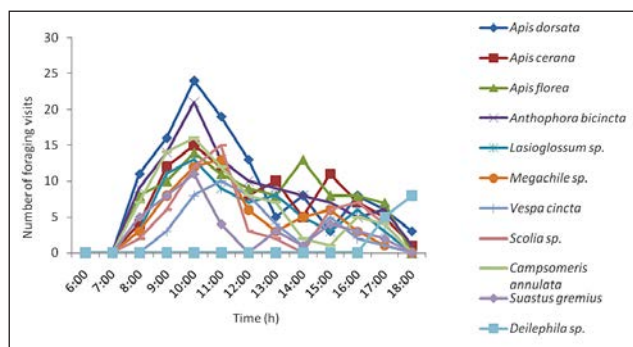


Fig. 6. Hourly foraging activity of insects on *Scaevola taccada*.

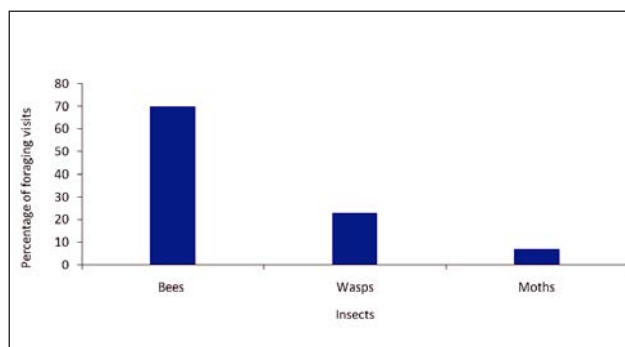


Fig. 7. Percentage of foraging activity of insects on *Scaevola taccada*.

found to have a little role in effecting pollination. All other insect species always brushed against the stylar cup nototribically, which resulted in the deposition of pollen precisely on the back of the thorax, abdomen and even wings. While leaving the flower, their back was also brushed against the stylar cup effecting pollen transfer unto the head and thorax. The forage collection behaviour showed that the *Apis* bees, wasps and moths were instrumental in effecting pollination, while other bees were only nectar robbers. Body washings of pollinating insects showed that *A. dorsata* and *A. cerana* carried more pollen, followed by wasps and then by moths (Table 3). Among pollinating bees, *A. dorsata* and all wasps spent 2–4 seconds at each flower in the forenoon and 4–7 seconds in the afternoon period. The moth, *Deilephila* sp., spent 2–3 seconds at each flower during its foraging confined to late evening hours. *S. gremius* spent 3–6 seconds at each flower in the forenoon and 4–7 seconds in the afternoon period. Among pollinating insects, *A. dorsata*, *A. cerana*, wasps, and *Deilephila* were swift fliers and quickly hopped from flower to flower on the same and on different plants, and thus they were regarded as effective pollinators in both cross- and self-pollination. However, the latter species was considered a minor pollinator due to its occasional foraging visits to the flow-

ers. Apart from these insects, the ant, *Camponotus* sp., was also observed collecting nectar from the flowers. It was a resident forager crawling and visiting the flowers all day, without any contact with the stylar cup and, hence, was regarded as nectar robber.

### Fruiting ecology and seed dispersal

In fertilized flowers, the calyx expands and bulges to accommodate the growing fruit. Fruits mature in about four weeks; they are initially green and creamy-white when mature. The fruit is a spherical fleshy drupe with thin epicarp, a thick corky mesocarp of air-filled parenchyma cells, and a thick, stone-hard endocarp, which represents the C-morph type: it is 15–20 mm long and 8–12 mm wide and crowned with calyx lobes (Fig. 5a). It is indehiscent and produces a light-weight brownish and ridged buoyant seed. Furthermore, fruits with very thin pulpy epicarp and a stone-hard endocarp of the seed were very seldom produced on the same plant, which represent the NC-morph type (Fig. 5b). The C-morph fruits can float in sea water and thus can be dispersed by ocean currents. Seeds which fall and reach the ground germinate quickly, produce seedlings and, subsequently, new plants. The NC-morph fruit dispersal was not observed, as such morphs were seldom produced by the plant. In the study area, the stem cuttings were used for *S. taccada* plantation along the shoreline as an effective sand binder and for beautification of the coastal area (Figs 1a,b; 5c,f).

### Discussion

*Scaevola taccada* is a large bushy evergreen shrub, which grows in coastal areas, especially on sandy and pebbly soils exposed to salt spray from the sea. Sutar

Table 3. Pollen recorded in the body washings of insects on *Scaevola taccada*.

| Insect species              | Sample size (N) | Number of pollen grains |       |      |
|-----------------------------|-----------------|-------------------------|-------|------|
|                             |                 | Range                   | Mean  | S.D. |
| <i>Apis dorsata</i>         | 10              | 61–342                  | 164.9 | 77.2 |
| <i>Apis cerana</i>          | 10              | 34–235                  | 125.4 | 49.2 |
| <i>Vespa bicincta</i>       | 10              | 17–98                   | 68.3  | 20.8 |
| <i>Scolia</i> sp.           | 10              | 13–126                  | 91.4  | 31.0 |
| <i>Campsomeris annulata</i> | 10              | 15–108                  | 61.4  | 22.9 |
| <i>Suastus gremius</i>      | 10              | 10–41                   | 27.2  | 7.7  |
| <i>Deilephila</i> sp.       | 10              | 06–32                   | 25.4  | 7.5  |

& al. (2017) reported that *S. taccada* flowers throughout the year. In this study, it was also found to flower throughout the year but concentrated flowering occurs only during the rainy season. The flowers produced in axillary cymes are covered by foliage; however, their pedicels and white corolla make them quite prominent against the foliage. The flowers are hermaphroditic, with bilateral symmetry, due to the position of all five petals on one side. Ewart (1930) noted that *Scaevola* species produce a short calyx, or it is totally absent. However, the present study shows that *S. taccada* has a well-developed calyx, which bulges and expands after fertilization acting as fruiting calyx. Ewart (1930) and Clarke & Lee (1987) mentioned that the mid-rib band of the central petal in *S. taccada* has a different colour from the other four petals. Twata (1990) and Howell & al. (1993) reported that *S. taccada* displays a colour contrast between the corolla throat and lobe, which attract insects to the stylar cup. In this study, it was found that in *S. taccada* all petals were milky-white, with yellowish tinge towards the throat of the corolla tube, fragrant, and the flowers produce nectar as an exclusive reward; the combination of these floral characters provide the visual, olfactory and biochemical cues for different categories of insects to visit the flowers.

The secondary pollen presentation has evolved for the promotion of cross-pollination in *Goodeniaceae* reported Leins & Erbar (1989), especially in the *Scaevola* genus, as mentioned by Ladd (1994) and Leins & Erbar (2006). These authors stated that relocation of pollen released from dehiscing anthers onto the stylar cup, which subsequently presents pollen for the pollination process, is a clear case of the secondary pollen presentation mechanism widely prevalent in the *Asteraceae* family. Howell (1995) reported that *Scaevola* flowers with the secondary pollen presentation mechanism avoid self-fertilization, even though the stigma is receptive during the male phase due to highly developed physiological, developmental and genetic barriers. However, the stigma is not available for cross-pollination because it is enclosed within the stylar cup and the flower enters the female phase when the stigma emerges from the stylar cup. He also stated that the *Scaevola* genus, with few exceptions, exhibits obligate exogamy as a function of strict sporophytic self-incompatibility. In this study, *S. taccada* is protandrous and slides the pollen mass from the dehiscent anthers into the stylar cup during mature bud

stage and then the stamens curl downwards and wither away. The stigma gradually pushes the pollen out from the stylar cup and eventually becomes receptive. Along with this, the stylar cup gradually attains downward orientation. During the period of developmental process of the stigma, the pollen is gradually exposed for brushing against the back of the probing foragers, in order to be transferred between flowers of the same or different plants. However, the pollen presentation mechanism facilitates pollen adherence to the stigma emerging from the stylar cup, which results in autogamy. Furthermore, this pollen presentation facilitates a greater accuracy in the pollen transfer than in the normal anther to stigma movement, and avoids interference between the male and female organs of the flower (Ladd 1994). Protandry, secondary pollen presentation and subsequent commencement of stigma receptivity exhibited by *S. taccada* suggest that the plant is principally out-crossing and pollinates by itself in if cross-pollination the event of failure of cross-pollination. This finding supports the report by Liao (2008) that *S. taccada* is xenogamous and has the potential for self-pollination. However, our study does not agree with this author's report that it essentially requires out-crossing to set fruits. In our breeding experiments, the fruit set was evidenced to a varying degree in both self- and cross-pollination. This study also reports that fruit abortion is quite significant in different self-pollination modes but it is totally absent in cross-pollination. This indicates that *S. taccada* has an inherent mechanism for eliminating selectively the genetically inferior fruits, in view of the availability of nutrients resulting from self-pollination through autogamy and geitonogamy. This finding is further supported by the fruit set rate in open pollinations and also by abortion at different stages of the fruit development. Furthermore, the plant produces characteristically 1-seeded fruits against four ovules produced by flowers. This could be attributed to space constraint for accommodation of more than one seed per fruit. This finding also strikes down certain reports posted on websites by anonymous authors that *S. taccada* flowers produce two seeds, one in each locule. Liao (2008) noted that *S. taccada* flowers last for approximately five days but in our study it was found that the stamens wither as soon as the anthers scoop the pollen mass into the stylar cup, while the corolla turns brown on the morning of the 3<sup>rd</sup> day and falls off mostly on the 4<sup>th</sup> day.

Different authors have reported the pollinators of *S. taccada* growing on the Hawaii Island. They say that it is mostly visited by bees (Gillett 1966; van Balgooy & Carolin 1975); pollinated frequently by non-native bees and less often by native bees, ants and small carpenter bees (Elmore 2008); pollinated mainly by bees and less often by ants and moths (Liao 2008). The last author also mentioned that the bees occasionally do not contact the stylar cup and, hence, act as nectar robbers. Furthermore, other insects avoid the corolla fan and visit the flowers from the back, most likely acting as nectar robbers. In this study, *S. taccada* was visited by bees, wasps and moths. However, it was principally pollinated by the bees *A. dorsata* and *A. cerana* and all wasps, which are regular and consistent pollinators and effect cross- and self-pollination. The moths act as minor pollinators as they visit the flowers occasionally. All these pollinators probe the flowers legitimately from the front side by landing on the corolla fan for nectar collection. During this process, the stylar cup with its hairs and bristles loaded with pollen brushes against the back of the pollinators effecting nototribic pollination. This mode of pollination has reportedly evolved for protecting pollen against pollen-collecting bees. It saves the pollen deposited on the back of the pollinator for its original purpose and also impedes access of pollinators for grooming by their legs, in order to maximize pollination rate, especially cross-pollination (Claßen-Bockhoff 2007). Mention deserves the fact that the pollinating bees and wasps have never attempted to collect pollen from the stylar cup, which suggests that they use *S. taccada* flowers as a source of nectar only. Furthermore, all other bees and the ant *Camponotus* sp. also use the flowers as a nectar source, although *Megachile* spp. occasionally attempt to collect pollen from the stylar cup. These insects act as mere nectar robbers depleting the nectar meant for pollinating insects. However, their nectar-robbing activity supposedly drives the pollinator insects to pay multiple visits to the flowers, thus promoting pollination, and especially exogamy.

Liao (2008) reported that *S. taccada* with its distribution in coastal areas, especially along the shoreline, is open to high winds. Wind speed is a significant factor and affects the visitation rate of the pollinators, which decrease with the increase in wind speed. High wind speeds prevent the pollinators from landing on a flower or blow them away from the forage source. In this study, *S. taccada* growing along the shoreline

with massive flowering during rainy season serves as an important source of nectar for different insects. High winds or wind speed did not deter insect foragers to visit the flowers as the latter are partially covered by the foliage and provide the necessary protection against the wind during forage collection. Furthermore, the shoreline is also fenced off with this plant by using stem cuttings. Therefore, in the study area *S. taccada* does not experience pollinator shortage and reproduces sexually to the possible extent by using the nutrient resources available in the sandy soils.

Seed heteromorphy defined as production of different types of seeds by a single individual appears in many species of angiosperms (Matilla & al. 2005). Heteromorphy in seeds may affect the physiological properties, as it is associated with ecological strategies that have evolutionary significance, including dormancy (Duran & Retamal 1989), germination and longevity (Diederichsen & Jones-Flory 2005). Production of heteromorphic seeds is one of the most effective strategies for adaptation and increasing the reproductive success of plants (Harper 1977). In *Amaranthaceae*, most of the species produce dimorphic seeds, which differ in germination characteristics and ability to tolerate salinity. In *Asteraceae*, *Bidens pilosa* produces dimorphic cypselas (seeds) from the disc florets of the same capitulum and these seeds have different dispersal abilities (Usharani & Solomon Raju 2018a). In *Synedrella nodiflora*, dimorphic seeds are produced from ray and disc florets of the same capitulum. Those produced from ray florets are adapted for short-distance dispersal, while those produced from disc florets are adapted for long-distance dispersal (Usharani & Solomon Raju 2018b). Emura & al. (2014) reported that *Scaevola taccada* distributed on the Okinawan Islands of Japan produces dimorphic seeds from different individual plants but this dimorphism occurs only in the internal structure of fruits and, hence, is not distinguishable by appearance. One fruit type has endocarps consisting of cork and thin pulpy layer (C-morph), which is adapted for dispersal by ocean water, while the other type has only pulp (NC-morph), which is adapted for dispersal principally by frugivorous birds. These authors also stated that the C-morph is dominant on beaches, whereas the NC-morph is more frequent on cliffs. The present study shows that *S. taccada* produces usually indehiscent C-morph fruits, with a thick pulpy epicarp, a thick corky mesocarp and a stone-hard endocarp of the seed. In spite of the presence of different

species of passerine birds in the study area, they never visited the plant for fruits and, hence, the plant is not ornithochorous. Fruits float and are dispersed by the ocean currents suggesting that the plant is hydrochorous (Carlquist 1965; Lesko & Walker 1969; Sutar & al. 2017). Fruits fallen on the sandy beach and reaching the beach anchor to the sandy soils germinate and produce new plants, but our field observations indicated that very few seeds have produced new plants. This study has testified that *S. taccada* produces very seldom NC-morph fruits with very thin pulpy epicarp and a stone-hard endocarp of the seed along with C-morph fruits on the same individual plant. This suggests that production of dimorphic fruits by different individuals at Okinawan coast, as reported by Emura & al. (2014), is an evolved character prompted by the habitat of the plant, so as to ensure reproductive success through seed. The C-morph fruits of *S. taccada* are fit for reproduction at this coast, while the NC-morph fruits are not adaptive there but the plant still keeps this trait as functional at the lowest level.

Elmore (2008) reported *S. taccada* as an invasive species, affecting the sexual reproduction and population build up by its sister species, *S. plumieri*. Since the plant with protandry and facultative xenogamy has the ability to outcross through vector-mediated pollination and self-reproduce by autogamy, it colonizes and establishes well on shorelines (Liao 2008). It also has the ability to extend its population vegetatively by roots occurring at certain nodes of the branches, which touch the ground. Locals reported that the stem cuttings, when planted, begin to produce new shoots and leaves within 15–20 days and are used to develop the coastal vegetation. Field observations showed that *S. taccada* was planted along the shoreline in the study area for beach stabilization, prevention of coastal erosion and landscaping. Therefore, *S. taccada* is an excellent species for coastal plantation and beautification of the shoreline, as long as it is not invasive to affect other local coastal species.

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