POLLINATION ECOLOGY OF *HIBISCUS TILIACEUS* L. (MALVACEAE), AN EVERGREEN TREE SPECIES VALUABLE IN COASTAL AND INLAND ECO-RESTORATION

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ABSTRACT

Hibiscus tiliaceus is an amphibious evergreen tree species which grows naturally in coastal and terrestrial habitats. Flowering and fruiting is mostly seasonal. It is self-compatible, protandrous, ambophilous involving melittophily and anemophily, and hydrochorous. Melittophily involves certain bees, which effect sternotribic pollination. Anemophily is functional only during the afternoon period. Delayed autonomous autogamy, a characteristic of the Malvaceae family, is not functional in this species. The tree has dual modes of regeneration, by seed and by sprouting prostrate stems. It is a most suitable species for coastal and inland eco-restoration.

ZUSAMMENFASSUNG: Bestäubungsökologie der immergrünen Baumart *Hybiscus tiliaceus* L. (Malvaceae), von Bedeutung für ökologische Renaturierung an Küsten und im Binnenland.

Hibiscus tiliaceus ist eine amphibische immergrüne Baumart, die natürlicher Weise an Küsten- und in Landlebensräumen wächst. Blüte und Früchte sind meistens saisonal. Sie ist selbstverträglich, protandrisch, ambophil, melittophil, anemophil und hydrochor. Die Melittophilie betrifft bestimmte Bienenarten, die sternotribische Bestäubungzur Folge haben. Die Anemophilie funktioniert nur während des Nachmittags. Verzögerte Selbstbestäubung, ein Merkmal der Malvaceaen, funktioniert nicht bei dieser Art. Der Baum hat zwei Arten von Regeneration und zwar durch Samen und durch Sprießen von Stängeln. Es ist eine sehr wertvolle Art für die ökologische Renaturierung der Küsten-und des nahen Binnenlandes.

REZUMAT: Ecologia polenizării la *Hybiscus tiliaceus* L. (Malvaceae), specie arboricolă sempervirescentă de importanță pentru refacerea ecologică a coastelor și a ariilor terestre.

Hibiscus tiliaceus este o specie arboricolă perenă amfibie, care crește în mod natural în habitate costiere și terestre. Înflorirea și fructificarea este, de obicei, sezonieră. Este auto-compatibilă, protandrică, ambofilă, care include melitofilie, anemofilie și hidrochorie. Melitofilia este caracteristică pentru anumite albine, care influențează polenizarea sternotribică. Anemofilia funcționează doar după-amiaza. Autogamia autonomă întârziată, caracteristică pentru familia Malvaceae nu funcționează la această specie. Arborele are două modalități de regenerare și anume, prin semințe și prin lăstărirea tulpinilor. Este o specie ideală pentru refacerea ecologică a zonelor costiere și terestre interioare.

INTRODUCTION

Pollination enables fertilization and seed production but its occurrence is largely dependent on external agents such as animals and wind (Maddala and Aluri, 2019). However, plants themselves resort to self-pollination having failed to achieve pollination by external agents (Barrows, 2011). Pollination ecology data are critical in dealing with effects of human changes to the habitats of plants (Hopper and Burbidge, 1986; Brown et al., 1997). Therefore, pollination ecology is most vital for seed production and subsequent recruitment of offspring and expansion of distribution of individual plant species in a variety of suitable habitats.

The genus *Hibiscus* comprises 200-300 species, distributed chiefly in tropical and subtropical regions (Pfeil et al., 2002). Of these, some species occur in open habitats along riverbanks and in freshwater wetlands, while others occur along brackish tidal and coastal wetlands (Tomlinson, 1986). *Hibiscus tiliaceus* is a pantropical coastal tree that extends to the tidal zone, inhabiting highly contrasting littoral and terrestrial habitats (Tomlinson, 1986). Wang and Wang (1999) noted that this tree species occurs commonly along the seashore, where the substrate salinity is relatively high. Santiago et al. (2000) noted that *H. tiliaceus* occurs in the most landward fringe of mangrove forests and also grows along freshwater streams or in upland forests, where soil salinity is negligible. Tang et al. (2011) reported that estuarine populations of *H. tiliaceus* are genetically more variable than the inland populations. This genetic diversity is correlated with population size; the estuarine populations do not consistently have a greater population size than the inland populations. Genetic variation in estuarine populations has been related to migrant sea-drift seed dispersal because the possibility for this form of seed dispersal is quite extensive in estuarine zones.

In Malvaceae, the flowers are hermaphroditic and entomophilous (Tang et al., 2007). Wind pollination is unlikely, as the pollen grains are sticky and tend to clump together (Spira, 1989). Most Malvaceae are self-compatible and capable of delayed selfing, having flowers with styles that are surrounded by and extend beyond monadelphus stamens (Klips and Snow, 1997; Kumar et al., 2014). In these species, the styles curve out and backwards as flowers age, until the stigmas contact pollen located in the upper anthers (Kumar et al., 2014).

Few data are available on *Hibiscus* pollination ecology. Buttrose et al. (1977) noted that *H. trionum* uses stylar movements as a mechanism to facilitate self pollination as an option if cross-pollination is failed. Willemstein (1987) noted that *H. trionum* is mainly pollinated by higher bees and pollen-feeding flies but, it is melittophilous. *H. laevis* is self-compatible (Klips and Snow, 1997) and uses stylar movements as a mechanism to foster out-crossing by putting the stigmas in the flight path of nectar-seeking bees subsequent to a predominantly male phase of anthesis during which the stigmas are held together and project forward (Stephens, 1948). This species is pollinated by bumblebees and oligolectic bees (Ruan, 2010). *H. moscheutos* is self-compatible and herkogamous, preventing self-pollination but not geitonogamy (Spira, 1989). The pollinators use petals as a cue to locate the flowers of *H. moscheutos* and the plant is pollinated by anthophorid bees and bumblebees (Snow and Spira, 1993; Kodoh and Wigham, 1998). *H. tiliaceus* is pollinated by an endemic Galapagos carpenter bee, *Xylocopa darwini*, which also nests in this tree (Williams, 1926). This carpenter bee pollinates *H. tiliaceus* in the littoral of the Galapagos (McMullen, 1989). Later, Hamrick and Godt (1990) noted that *H. tiliaceus* is insect-pollinated. The data on the pollination ecology of *Hibiscus* is incomplete to understand the sexual reproduction, starting from the floral biology to seed dispersal and regeneration. With this background and absence of pollination studies on *H. tiliaceus* in India, the present study has been carried out to provide details of the pollination ecology of *H. tiliaceus* to enable other reaserchers to take up similar work in the entire range of this species for its use in coastal eco-restoration projects.

MATERIAL AND METHODS

H. tiliaceus trees growing along the coastlines and in inland terrestrial sites in Visakhapatnam, Andhra Pradesh, S.E. India (17°42'N Latitude and 82°18'E Longitude) were selected for the study during June 2018-May 2019.

Regular visits to these trees were made to record flowering and fruiting seasons. Ten inflorescences, which were about to initiate flowering on five plants were tagged and followed to record the flower-opening schedule and the timing and mode of anther dehiscence. Anther dehiscence timing was confirmed by observing the anthers, under a 10x hand lens. Twenty fresh flowers were used to record the floral morphological aspects, flower type, sex, shape, colour, symmetry, calyx, corolla, stamens, ovary, style and stigma. The floral configuration and rewards presentation aspects were observed in relation to the probing and forage collection of activities of insects. Ten mature buds two each on five plants were bagged and tagged to measure nectar volume and sugar concentration using the protocols provided by Dafni et al. (2005). The micropipette was inserted into the flower base to extract nectar for measurement. The average nectar of ten flowers was taken as the total volume of nectar/flower and expressed in µl. Hand Sugar Refractometer (Erma, Japan) was used for this purpose. Nectar analysis for sugar types was performed as per the Paper Chromatography method described by Dafni et al. (2005). The stigma receptivity was observed visually and by H_2O_2 test. In visual method, the stigma physical state was considered to record its receptivity duration. H_2O_2 test as given in Dafni et al. (2005) was followed for the confirmation of the stigma receptivity period. Insects foraging at the flowers were observed throughout the day on three different days for their mode of approach, landing, probing behaviour and contact with the floral sexual organs. Fruit maturation period, the fruit and seed characteristics were recorded. Field observations were made to record fruit/seed dispersal mode. Casual observations were also made to record whether the seeds after their dispersal germinate immediately or not.

RESULTS

H. tiliaceus is a coastal, fast-growing evergreen tree that occurs along the shoreline and in the landward fringe of mangrove forest, where soil salinity varies from high to low and along freshwater streams, where soil salinity is negligible (Fig. 1a). It regenerates quickly from branches that touch the soil and form roots. It also propagates through seed, which is produced from sexual reproduction. The plants produced from vegetative propagation bloom within a year, while those produced from seeds bloom in the second or third year depending on the habitat where they grow. Field observations along the coastline showed that this tree is important for the stabilization of sand dunes and coastal wind breaks and as a living fence post. Furthermore, it is also cultivated in inland garden landscapes as an ornamental tree for shade purposes. It produces a short trunk with several twisted and spreading branches, forming impassable thicket. The leaves are simple, alternate, heart-shaped, wavy and slightly hairy, with leaf-like stipules at the base of the petiole (Fig. 1b).

The plant flowers from October to January, but sporadic flowering occurs throughout the year (Fig. 1c). The flowers are borne in three- to six-flowered cymes and occasionally are solitary in axillary and terminal positions. The buds stay almost erect during the mature and immature stages, and attain a down-hanging position upon anthesis and stay away from the foliage, without any contact between flowers and leaves. They are bright yellow, showy, large, hermaphroditic and fragile, and they fall at the end of the same day on which they open. Individual flowers are pedicellate, cup-shaped, with the calyx consisting of five elongatetriangular light greenish sepals and corolla consisting of five radiating obovate free petals four-six cm long, with a dark maroon base on the inside and basally adnate to the staminal tube. The staminal column is a monadelphous tube consisting of numerous united filaments basally and protruding, with low and high one-celled anthers having yellow spiny pollen; it is inserted in the centre of the flower. The most distal part of the staminal column has a red, five-partite slender style each branch terminated with a capitate stigma. The ovary is five-celled, but each cell has a false septum, making it altogether 10-celled, and each cell contains many ovules.

Mature buds open at 07,00-08,30 hrs (Figs. 1d-h). The staminal column with stamens positioned below the five-partite style segregates male and female sex organs and characterizes herkogamy. The anthers dehisce at the time of unfolding of the petals and the pollen at that time is sticky, (Fig. 1i) but it becomes dry and powdery around midday. The stigmas are receptive after anthesis and remain so, until flower fall; they are held together and stay erect, or slightly open up in a columnar form until flower fall (Figs. 1j-k). Individual flowers secrete 0.2-0.3 µl of nectar, with 28-32% sugar concentration. The flowers fade gradually from yellow to light pink towards evening and fall off without closing. The corolla, stamen-tube and upper portion of the gynoecium fall off as a single unit, while the calyx and ovary remain in place after pollination (Fig. 1l).

Figure 1: *Hibiscus tiliaceus*: a. Habit; b. Alternate leaf arrangement and leaf-like stipules at the base of the petiole; c. Flowering phase; d.-e. Buds; f.-h. Stages of anthesis; i. Height of staminal column against petals; j. Staminal column with dehisced stamens and five stigmas held together projecting forward; k. Staminal column with dehisced anthers and slightly stretched out stigmas; l. Calyx with ovary after fall of corolla together with staminal column and upper portion of gynoecium; m.-n. Initial stages of fruit development.

The showy hanging flowers against the background of green foliage are very attractive to floral visitors. The flowers were foraged by various bees – honey bees (*Apis dorsata, A. cerana, A. florea*, and *Trigona iridipennis*), carpenter bees (*Xylocopa latipes* and *Ceratina simillima*) and leaf-cutter bees (*Megachile* sp.). Of these, *X. latipes* foraged for only nectar, while all others foraged for both nectar and pollen. Their foraging intensity was found to be dependent on the number of flowers available on any given day. The bees usually landed on upturned stigmas, and then moved towards the base of the flower by walking through the pollen-laden anthers to probe for nectar and simultaneously, they collected pollen. The dark maroon corolla base appeared to be serving as nectar guide, to guide the bees to access nectar. After forage collection, they departed from the flower by walking on the petals without touching the stigmas again. In this flower-probing behaviour, if the bees carried pollen from the previously visited flower, then they transferred it to the stigmas effecting cross-pollination. Their first visits to flowers made them as pollen carriers only without effecting pollination. Occasionally, the bees, especially *A. florea* and *T. iridipennis*, landed on the petals and walked towards the flower base to collect nectar and after its collection, they made a U-turn and walked on the staminal column to collect pollen; then they departed from the flower with or without touching the stigmas. In these foraging behaviours, the bees contacted the pollen with their ventral side effecting sternotribic pollination.

Wind shakes the branches of the tree, causing the dry and powdery pollen available in flowers around midday to fall on the stigmas of the same flowers, easily effecting self-pollination due to the hanging position of flowers. Depending on the wind speed, which is very high at certain times along the coast, some of this dispersed pollen could reach the stigmas of other flowers of the same or different conspecific plant to effect cross-pollination.

The fruit is an ovoid to ellipsoid, light brown dry loculicidal capsule 2.5-3 cm long, with 30-50 seeds. Fruits mature within 5-7 weeks after pollination (Fig. 1l-m) and split apart into five two-celled segments to release seeds (Figs. 2a.-b.). However, the calyx and involucre remain attached with some leftover seed which could not be dispersed or had fallen to the ground by gravity (Fig. 2c). Seed are brownish-black, rough-coated, 4 x 2 mm and hairless; they are dispersed in inland habitats by rainwater during the rainy season and float in seawater, remaining viable for more than three months. The air space within the thick water-impermeable seed coat enables the seeds to float. In inland habitats, seeds germinate during the rainy season and produce new plants.

Figure 2: *Hibiscus tiliaceus:* a.-b. Loculicidal capsule dehiscence and seed dispersal; c. Capsule still in place after seed dispersal.

DISCUSSION

The genus *Hibiscus* is chiefly tropical and subtropical in distribution. Its species occur either in open habitats along riverbanks and in freshwater wetlands, or in brackish tidal and coastal wetlands (Pfeil et al., 2002). *H. tiliaceaus* grows in littoral and terrestrial habitats (Tomlinson, 1986), along the seashore habitats, where the substrate salinity is relatively high (Wang and Wang, 1999), in the most landward fringe of mangrove forests and along freshwater streams or in upland forests, where soil salinity is negligible (Santiago et al., 2000). Furthermore, in this species estuarine populations have been reported to be tolerant to high salinity compared to upland populations (Santiago et al., 2000). Estuarine populations are small and are genetically more variable than the large inland populations, and this genetic variation in estuarine populations is linked to migrant sea-drift seed dispersal, because this form of dispersal is quite extensive here (Tang et al., 2011). The present study showed that *H. tiliaceus* grows naturally in coastal and inland wetlands as well as inland terrestrial habitats where it is usually cultivated as an ornamental tree, indicating that it is a highly versatile species to grow in both saline and non-saline habitats.

Most Malvaceae species are self-compatible and produce flowers with a monadelphous staminal tube consisting of numerous stamens, all of which, along with the style extend beyond the tube. The style is usually five-partite and each branch has a capitate stigma (Klips and Snow, 1997; Kumar et al., 2014). The styles with stigmas are held together and project forward facilitating nectar-seeking foragers to contact the stigmas first and then pass through the stamens with dehisced anthers to achieve cross-pollination. The stigmas that were not pollinated will curve out and reflex backwards to touch the upper anthers situated below to achieve selfing. This stylar movement is shown as a delayed autonomous selfing mechanism which occurs only when all opportunities for cross-pollination have passed and hence it is a fail-safe mechanism to ensure selfing in the absence of pollinators (Stephens, 1948; Klips and Snow, 1997; Kumar et al., 2014). Delayed autonomous selfing occurs in several genera of Malvaceae (Ruan et al., 2011) such as in *H. laevis* and *H. trionum* (Buttrose et al., 1977) and *H. laevis* (Stephens, 1948; Klips and Snow, 1997). The present study found that *H. tiliaceus* does not exhibit delayed selfing mechanism as the stigmas are held together and project forward through the life of the flower. The absence of mechanism of stylar curvature and movement provides equal opportunities for both cross- and self-pollination. Further, the flowers last only one day and the corolla, staminal tube and upper portion of the gynoecium fall off as a single unit in both pollinated and un-pollinated flowers, indicating that pollen tube growth through the stylar tissue is very fast to fertilize the ovules in pollinated flowers.

In Malvaceae, the flowers are hermaphroditic and entomophilous (Tang et al., 2007); pollinators include generalized pollination insects, bees and butterflies (Kodoh and Wigham, 1998). *H. trionum* is pollinated by honey bees (Willemstein, 1987), *H. laevis* by bumblebees and oligolectic bees (Ruan, 2010), and *H. moscheutos* by solitary anthophorid bees and bumblebees (Snow and Spira, 1993). In *H. moscheutos*, pollinators use petals as cue to locate the flowers (Kodoh and Wigham, 1998). *H. tiliaceus* wood is used by the carpenter bee *Xylocopa darwini*, for its nesting (Williams, 1926) and is also pollinated by the same bee in the littoral zone of the volcanic Galapagos Archipelago (McMullen, 1989). In the present study, *H. tiliaceus* flowers are bright yellow and seem to serve as a cue for the pollinating bees to locate and probe the flowers for nectar and/or pollen. The pollinators include nectar- and pollen-collecting honey bees, leaf-cutter bees and nectar-collecting carpenter bees. The bees that proceed by contacting the stigmas first and then pollen to collect pollen and nectar; this way of flower probing ensures the occurrence of cross-pollination while those that proceed skipping the staminal column to collect nectar and then pollen by walking on the staminal column may or may not effect selfing. In either way, the bees effect sternotribic pollination which involves wastage of pollen during flight and loss of pollen due to their grooming. However, this pollen loss is compensated by the production of copious pollen by individual flowers.

In Malvaceae, wind pollination is unlikely because pollen grains are sticky and tend to clump together (Spira, 1989). In *Kosteletzkya virginica*, self-pollination occurs by wind brush pollination when there is wind. When the wind shakes the branches with open flowers, contact between leaves and pollen leads some pollen to stay on the surface of leaves; after this, wind flaps the branches easily to make stigmas to touch this pollen, achieving self-pollination (Ruan, 2010). In the present study, it has been found that *H. tiliaceus* pollen is sticky initially, but gradually becomes dry and powdery around midday. Winds of various speeds facilitate pollen shedding from the anthers easily from midday and until the flowers fall and it is captured by the capitate stigmas due to its down-hanging position and achieves selfing. The spiny nature of pollen facilitates the stigmas to hold the pollen intact, ensuring pollen germination and subsequent fertilization prior to flower drop. Therefore, *H. tiliaceus* is also anemophilous, but it is largely useful for the occurrence of selfing.

Hibiscus is hydrochorous (Tomlinson, 1986). The seeds float for a few months and have dispersal potential over long distances. *H. hamabo* produces buoyant seeds which float for a long period (Nakanishi, 1988). *H. moscheutos* produces seeds which are initially dispersed by gravity and then secondarily by water during floods (Kudoh et al., 2006). In *H. tiliaceus*, the seeds float, withstand immersion in seawater and remain viable for more than three months. Its widespread distribution is attributed to seed dispersal by ocean currents (Nakanishi, 1988). The present study shows that *H. tiliaceaus* disperses seeds by splitting open of the loculicidal capsule, but it is not very effective since some seed remain attached to the vertical septa in split capsules which do not detach after their maturity and splitting. The seeds dispersed from the capsules fall to the ground by gravity and are subsequently carried away by seawater in plants along the coastline and by rainwater in plants growing in inland areas. This mode of seed dispersal indicates that seawater or freshwater is an effective medium for its widespread distribution. Further, the seed are buoyant because of the airspace inside the thick water-impermeable seed coat and remain viable for a long period during dispersal and until they find a suitable substrate for germination and growth of new plants. In inland habitats, *H. tiliaceus* does not have the opportunity to float in freshwater all the time as rains are seasonal in occurrence. In effect, the plants growing in such habitats are most likely to produce non-buoyant seeds by simply losing the airspace and having a thin water-permeable seed coat for germination in terrestrial habitats. This hypothesis is in line with the report by Kudoh et al. (2006) that *H. tiliaceus* adapted to inland habitats of the Bonin Islands produces non-buoyant seed which do not float on sea water. Furthermore, these authors noted that the immigrants of this species adapted to inland island habitats have evolved various modifications to their features to produce a new species, *H. glaber*, endemic to the islands.

Chin and Enoch (1988) reported that *H. tiliaceus* is wind- and salt-resistant and adapted to a wide range of environments. It is used for the stabilization of sand dunes and the formation of coastal wind breaks. Tang et al. (2003) mentioned that it is often cultivated inland in garden landscapes as an ornamental shade tree. The present study also reports that *H. tiliaceus* is an important evergreen tree species for coastline restoration due to its multiple uses. Since this tree species has the ability to propagate through seed and by sprouting prostrate stems, it is a most suitable species for use in eco-restoration projects for the restitution of ecologically degraded, damaged and destroyed coastal and inland ecosystems.

CONCLUSIONS

Hibiscus tiliaceus is a fast growing evergreen tree species that grows both in coastal and inland habitats. It is largely a seasonal flowerer and produces large hermaphroditic cup-shaped flowers, which are quite attractive against the background foliage. It is self-compatible, protrandrous, melittophilous, anemophilous, and hydrochorous. Its dual regeneration ability through seed and by sprouting prostrate stems ensures its widespread distribution. Further, it is an important tree species in the eco-restoration of ecologically deteriorated coastal and inland habitats.

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