ARTICLE

ON THE REPRODUCTIVE ECOLOGY OF *SUAEDA MARITIMA*, *S. MONOICA* AND *S. NUDIFLORA* (CHENOPODIACEAE)

A.J. Solomon Raju & Rajendra Kumar

Partner

zoo*h!*
ZÜRICH

Publisher/Host

WILD ZOO
Threatened Taxa

On the reproductive ecology of *Suaeda maritima, S. monoica* and *S. nudiflora* (Chenopodiaceae)

A.J. Solomon Raju [1] & Rajendra Kumar [2]

[1]Department of Environmental Sciences, Andhra University, Visakhapatnam, Andhra Pradesh 530003, India
[2]Ministry of Environment, Forest and Climate Change, Indira Paryavaran Bhavan, Jorbagh Road, New Delhi 110003, India
[1]ajsraju@yahoo.com (corresponding author) [2]kumar.rajendra@gov.in

Abstract: Floral biology, sexual system, breeding system, pollinators, fruiting and seed dispersal aspects of three *Suaeda* species, *S. maritima, S. monoica* and *S. nudiflora* (Chenopodiaceae) were studied. The flowers of all the three species are hermaphroditic, dichogamous, strongly protogynous with a pistillage phase during the mature bud stage and staminate phase following anthesis, self-compatible exhibiting mixed breeding systems with special adaptation for cross-pollination; but both self- and cross-pollination are vector-dependent. In all, the flowers display a mix of anemophilous and entomophilous traits. Anemophily is effective in high salt marshes while water currents bring about pollination in low salt marshes; insects pollinate the flowers while collecting the forage from pistillate and staminate phase flowers. In these species, the whole plant breaks off and rolls on the floor while shedding its diaspores. Fruits with seeds intact and/or seeds shed from fruits float on water due to their ability for buoyancy. The fruits and seeds thus disperse, settle in the entire extent of salt marshes or coastal areas and germinate in mid-summer season when salinity is very high in high and low salt marshes.

Keywords: Anemophily, entomophily, hydrophily, seed dispersal, *Suaeda.*

INTRODUCTION

The genus *Suaeda* consists of 110 species all over the coastal tropics and sub-tropics of the world (Gelin et al. 2003). It consists mostly of halophytic leaf-succulents that grow in saline and alkaline wetlands and deserts. A number of species are valuable as feed for livestock in arid areas while other species are useful to desalinize irrigated farmlands. This genus has both C_3 and C_4 photosynthetic pathways. It uses the C_4 photosynthetic pathway when exposed to a stressful environment and hence is an adaptive mechanism (Fisher et al. 1997). In central Asia, C_4 species of *Suaeda* are mostly annuals (Glagoleva et al. 1990). Both the C_3 and C_4 species of *Suaeda* commonly grow side by side; C_4 species grow abundantly in drier and more saline sites. They are enabled by their succulence to persist throughout the dry season. Wetson et al. (2012) stated that *S. maritima* is a widely occurring halophyte of salt marshes. These authors noted that high marsh and low marsh plants develop different morphologies as a result of different stressful soil conditions - small and less branched mature plants in low marshes and long and much-branched mature plants in high marshes. *S. maritima* is an annual obligate succulent halophytic annual mangrove herb and thrives in both coastal and inland salt marshes (Flowers et al. 1977). Two varieties, *S. maritima* ssp. *richii* and *S. maritima* ssp. *maritima* have been reported in Newfoundland and Nova Scotia in northern America; these varieties were classified based on growth habit and seed size. The former is small, procumbent and mat-forming with seeds 1–1.5 mm in diameter while the latter variety is prostrate to ascending with seeds 1.5–2 mm in diameter (Ferren & Schenk 2003). Three principal varieties were described in this species by Chapman (1947). They are var. *vulgaris, macrocarpa* and *flexilis*. var. *vulgaris* is a large plant with spreading branches suffused with red, and with leaves tapering slightly towards each end. The flowering occurs six months after seed germination; it occurs from August to October, the fruit is small, not exceeding 1.5mm diameter. var. *macrocarpa* is a decumbent or prostrate plant with divaricate branches and short leaves, occupies a higher zone. The flowering occurs 5 months after seed germination; it occurs from mid-July to September, and produces 2mm diameter fruits. var. *flexilis* is an erect short-stemmed plant with branches from the mid-part of the stem, occupies muddy soils. The flowering occurs 6 months after seed germination; it occurs in August–October and produces 1.1–1.4 mm diameter fruits. In all the three varieties, seed germination occurs from March onwards and fruits disperse from October onwards. Fruit dispersal occurs by tides and they can float for 3 days and then settle in the soil. Of these, var. *vulgaris* and var. *flexilis* have been reported to be widespread. var. *vulgaris* is recorded from Asia, France, Macronesia, the Mediterranean and Russia, the Caucasus; var. *macrocarpa* from Belgium, France, Spain and Russia; and var. *flexilis* from Sweden, Germany, Belgium, France, Spain and southern Europe. *S. maritima* is successful as a colonist of secondary bare areas and salt plans of higher marshes in both Europe and America. Chapman (1947) mentioned that *S. maritima* flowers are homogamous or feebly protandrous; autonomous autogamy is easily possible. The flowers are nectar-less and hence there were no insect visitors. The insects such as *Coleophora suaedivora* (Coleophoridae) and *Phthozimaea suaedella* (Gelechidae) feed on leaves and seeds. Bassett & Crompton (2011) recorded that *S. maritima* flowers during July–September and is wind-pollinated. Naskar & Mandal (1999) reported that *S. maritima* is pollinated by wind, water currents and flies. *S. monoica* is a salt marsh mangrove succulent annual herb similar to *S. maritima* (Ravikumar et al. 2011). It is a C_4 species and grows in hyper saline soils; the plants possessing the C_4 photosynthetic pathway grow abundantly in hot, dry, high-light environments (Shomer-Ilan et al. 1975; Ehleringer & Monson 1993). *S. nudiflora* is a salt mangrove succulent herb that grows well in the highly saline, dry and extreme high tidal belt. It has small, linear and succulent leaves and this succulence is a morphological adaptation. It is a C_4 plant (Singh et al. 2004; Patel & Pandey 2009). Dem'yanova (1977) worked on the flowering and pollination ecology of *S. microphylla, S. physophora, S. acuminata* and *S. linifolia* in the desert of the Ili valley in USSR. This author reported that these species are predominantly anemophilous and entomophilous but the latter has no significant importance. The flowers receive visits of *Halictus* bees during staminate phase by which time the stigma begins to wither and does not accept pollen. Keighery (1979) reported that honey bees and syrphid flies collect pollen from the flowers of *Suaeda australis*; but this author did not mention whether they are pollinators.

The work done so far on *Suaeda* species as stated above suggests that this genus as a mangrove associate has not been studied at all with reference to their reproductive ecology from the perspective of their importance in the mangrove ecosystem. It is in this context, *Suaeda maritima* (L.) Dum.*, S. monoica* Forsk. Ex. J.F. Gmel. and *S. nudiflora* (Willd.) Moq. (Chenopodiaceae) occurring in the Godavari-Coringa mangrove forest in the State of Andhra Pradesh, India, have been thoroughly studied for their floral biology, sexual system, breeding system,

floral rewards, pollinators and their foraging behaviour. Further, fruit and seed dispersal aspects have also been studied to the extent possible. The outcome of the work is considered to be immensely valuable for understanding the reproductive ecology of the studied *Suaeda* species and their potential use for the clean-up of salts from saline soils.

MATERIALS AND METHODS

Study area

The Godavari mangrove wetland lies between $16^0 30'$–$17^0 00'$N & $82^0 10'$–$80^0 23'$E in Andhra Pradesh State, India. In this wetland, three *Suaeda* species, *S. maritima, S. monoica* and *S. nudiflora* (Chenopodiaceae) occur with different population densities depending on soil conditions. All the three *Suaeda* species form thick mats in upper and low salt marshes in the estuarine area and towards land as well. *S. maritima* and *S. monoica* grow together successfully while *S. nudiflora* mostly in areas which are not occupied by the other *Suaeda* species. The locals use *Suaeda* species for treating certain skin diseases by external application. All the three *Suaeda* species were studied in detail for their reproductive ecology. Field studies and lab-work were undertaken from February 2011 to June 2014.

Flowering and floral biology

Flowering seasons were defined based on regular field trips made for three years. Observations regarding the organization of inflorescences, the spatial positioning of flowers, and their position (terminal, axillary, etc.) on the plants were made since these features are regarded as important for foraging and effecting pollination by flower-visitors. The flower life was recorded by marking 50 just anthesed flowers and following them until fall off. Anthesis was initially recorded by observing 50 marked mature buds in the field. Later, the observations were repeated 3 to 4 times on different days in order to provide accurate anthesis schedule for each species. Similarly, the 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 observing the anthers under a 10x hand lens. The details of flower morphology such as flower sex, shape, size, colour, odour, tepals, stamens and ovary were described based on 25 flowers randomly collected from a population of plants for each species. The order of wilting or dropping off of floral parts was recorded. Observations regarding the position and spatial relationships of stamens and stigma in mature bud, at anthesis and after during the flower-life with reference to self and/or cross-pollination were made very carefully.

Determination of pollen output

Twenty-five mature but undehisced anthers from five different plants were collected and placed in a petri dish. Later, a single anther was taken out and placed on a clean microscope slide (75x25 mm) and dabbed with a needle in a drop of lactophenol-aniline-blue. The anther tissue was then observed under the microscope for pollen, if any, and if pollen grains were not there, 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 (40x objective, 10x eye piece). This procedure was followed for counting the number of pollen grains in each anther collected. Based on these counts, the mean number of pollen produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers in the flower for obtaining the mean number of pollen grains per flower. The characteristics of pollen grains were also recorded.

Determination of pollen-ovule ratio

The pollen-ovule ratio was determined by dividing the average number of pollen grains per flower by the number of ovules per flower. The value thus obtained was taken as pollen-ovule ratio (Cruden 1977).

Examination of nectar characters

The presence of nectar was determined by observing the mature buds and open flowers. The flowers used for this purpose were bagged at the mature bud stage, opened after anthesis and squeezed nectar into a calibrated micropipette for measuring the volume of nectar. Then, the average volume of nectar per flower was determined and expressed in μl.

Determination of stigma receptivity

The stigma receptivity was observed visually and by H_2O_2 test. In the visual method, the stigma physical state (wet or dry) and the unfolding of its lobes were considered to record the commencement of receptivity; withering of the lobes was taken as loss of receptivity. H_2O_2 test as given in Dafni et al. (2005) was followed for noting stigma receptivity period. This test is widely followed although it does not indicate the exact location of the receptive area. In the present study, the period of slow release of bubbles from the surface of stigma following the application of hydrogen peroxide was taken as stigma receptivity.

Determination of natural fruit set

One hundred inflorescences were tagged on different plants prior to anthesis and followed for fruit and seed set rate in open-pollinations. Fruit maturation period, fruit dehiscence and seed dispersal aspects were observed in detail.

Observations of flower-visitors

The foraging activity of insects was observed from 06:00h to 18:00h. After making preliminary observations on the categories of flower visitors, a thorough knowledge of the local insect species was obtained by observing the representative species of insects available with the Pollination Ecology Laboratory in the Department of Environmental Sciences, Andhra University, Visakhapatnam. Some insect species were identified to genus level only and a few insect species could not be identified at all even by the Insect Taxonomic Group with the Division of Entomology, Indian Agricultural Research Institute, New Delhi. With the knowledge of local insect species, attempts were made to observe flower visitors on each plant species chosen for the study. The insect species were observed visually and by using binoculars; the insect species that could not be identified on the spot were captured and later identified with the help of the identified specimens available in the Department. The hourly foraging visits of each insect species on each plant species was recorded on 3 or 4 occasions depending on the possibility and the data was tabulated to use the same for further analysis. For each species, 15–20 inflorescences were selected to record the foraging visits of insects. The data obtained was used to calculate the percentage of foraging visits made by each insect species per day and also to calculate the percentage of foraging visits of each category of insects per day in order to understand the relative importance of each insect species or category of insects.

Determination of pollen carryover efficiency of insects

The flower visitors were captured during 10:00–12:00 h on each plant species and brought to the laboratory. For each insect species, 10 specimens were captured and each specimen was washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and observed under the microscope to count the number of pollen grains present. In case of pollen collecting insects, pollen loads on their corbiculae were separated prior to washing them. From this, the average number of pollen grains carried by each insect species was calculated to know the pollen carryover efficiency of different insect species.

Determination of foraging behaviour of insects

The foraging activity of insect species was confined to the daytime only. The insects were observed on a number of occasions on each plant species for their foraging behaviour such as mode of approach, landing, probing behaviour, the type of forage they collect, contact with essential organs to result in pollination, inter-plant foraging activity in terms of cross-pollination, etc. Observations were also made on the bud, flower and fruit feeding activity by insects.

Photography

Study area, habitat, plant, flower and fruit details together with insect foraging activity on the flowers were photographed with a Nikon D40X Digital SLR (10.1 pixel), a TZ240 Stereo Zoom Microscope and with an SP-350 Olympus Digital Camera (8.1 pixel). Olympus Binoculars (PX35 DPSR Model) were also used to make field observations. A Magnus Compound Microscope - 5x, 10x, 40x and 100x magnification was used for studying pollen characteristics.

RESULTS

Phenology

Suaeda maritima, S. monoica and *S. nudiflora* are halophytic succulent mangrove associates; the first two are erect glabrous annual herbs growing to a height of up to 0.3m while the last one is a perennial prostrate herb growing to a height of up to 1.5m tall. All the three species grow in high and low salt marshes and along tidal banks (Images 1, 7a). These three species invariably show different growth responses depending on the locality, high or low salt marshes. The growth forms could be distinguished, the one which grows in low marsh locality is smaller and less branched than the other one which grows in high marsh locality. In case of *S. maritima*, the plants that grow at high tide marsh without other species grow taller with many lateral branches. *S. maritima* and *S. monoica* usually form dense communities and are usually shiny light green in color, and turn reddish as they age. *S. nudiflora* grows in more widely spaced communities in relatively semi-dry areas, it tends to be grey in color, and turns blackish as it ages. The leaves are long and sickle-shaped when young, base truncate and apex acute in *S. maritima*; alternately crowded, linear-oblong, spathulate, flat, rounded at tip and narrowed at base in *S. monoica*; and linear, ovate, fleshy, terete base acute, apex sub-acute

Image 1. Habitat of *Suaeda* species - co-occurrence of *S. maritima*, *S. monoica* and *S. nudiflora*. © A.J. Solomon Raju.

globose-ellipsoid, exserted, introrse, dithecal and tetra-sporangiate in all the species (Image 3b). The staminal filaments are white and ban-shaped in *S. maritima* and *S. monoica* while they are light yellow and cylindrical in *S. nudiflora*; in all the three species, the filaments are soft and glabrous, and inserted near the tepal bases. In all the three species, ovary is pear-shaped, uni-locular with solitary ovule on basal placentation, 1mm long and 1mm wide, whitish green, succulent and glabrous (Images 3g, 8h,i, 12g,h). Stigmas are sessile, filiform, hairy-papillate, and arise from a pit at the top of the ovary; they are 3 in *S. maritima* (Image 3f) and *S. monoica* (Image 8f,g) and 2 in *S. nudiflora* (Image 12g).

in *S. nudiflora*. Seeds germinate in April and new plants mature to reproductive phase in three months and flower during July–October in *S. maritima* and *S. monoica* (Image 2a,b). In *S. nudiflora*, the flowering occurs throughout the year with concentrated flowering from July-September (Image 11a–c). Inflorescences are axillary in position and the flowers are clustered in cymes; the number of flowers at each leaf axil is 9–18 in *S. maritima* (Image 2c–e), 5–8 in *S. monoica* (Image 7b,c) and 2–4 in *S. nudiflora* (Image 11d).

Flower morphology

The flowers are green and erect in *S. maritima* and *S. monoica* while they are greenish-yellow and semi-erect in *S. nudiflora*. The flowers are bisexual in all the three species; they are 3mm long, 4mm wide in *S. maritima*, 2–3 mm long and 3mm wide in *S. monoica*, and 1–2 mm long and 2 mm wide in *S. nudiflora*. The flowers in all the three species have rosaceous perianth represented by five free equal succulent, glabrous and keeled lobes or tepals. The tepals are abaxially rounded and distally hooded at maturity. The stamens are 5, free, basifixed, the anthers

Floral biology

The flowers are open from 0800–1100 h in all the three species (Images 3a, 7d, 8a-d, 12a-d). In all, the papillate stigma lobes protrude out of the maturing (bulging) bud and are receptive a day before anthesis (Image 3e). The lobes gradually wither and become unreceptive by the time the anthers protrude due to the unfolding of the hooded perianth lobes during anthesis. The protruded stamens extend beyond the height of withered stigma lobes (Image 12e) and dehisce by longitudinal slits exposing the bright yellow colored and powdery pollen grains. In all the three species, the pollen grains are spheroidal, pantoporate, multiporate and vary in size; it is 25.5 ± 0.86 µm in *S. maritima* (Image 3c,d), 20.37 ± 1.22 µm in *S. monoica* (Image 8e) and 18.21 ± 0.29 µm in *S. nudiflora* (Image 12f). The pollen output per anther is 3,818 ± 28.34 in *S. maritima*, 3,253 ± 17.34 in *S. monoica* and 2,035 ± 21.23 in *S. nudiflora*. The pollen output per flower is 19,090 in *S. maritima*, 16,265 in *S. monoica* and 10,175 in *S. nudiflora*. The pollen-ovule ratio is equal to the pollen output per anther due to 1-ovuled flowers in all the three species. The flowers in all the species

Image 2. *Suaeda maritima*: a. & b - Vegetative phase; c–e - Inflorescence with buds and flowers. © A.J. Solomon Raju.

Image 3. *Suaeda maritima*: a - Mature bud; b - Stamens; c & d - Pollen grains; e - Mature bud exposing the trifid stigma; f - Style with trifid stigma; g - Ovule; h - Fruit; i - Seed. © A.J. Solomon Raju.

produce 1.2 ± 0.21 µl of nectar; it is available only during the staminate phase. In these species, the perianth lobes close back and cover the ovary but not the anthers by the evening of the 2nd day. The stamens fall off subsequently on the 3rd or 4th day. The flower life is 3–4 days. The perianth lobes gradually bulge along with the growing seed, and hence the perianth acts as seed cover.

Breeding behavior

In all the three species, the flowers are strikingly protogynous, the mature bud stage is pistillate due to the protrusion and receptivity of stigmatic lobes while the post-anthesis stage is staminate due to cessation of stigma receptivity by the time of anthesis and dehiscence of anthers after anthesis. The pistillate and staminate phases are therefore temporally separated and this situation is a type of temporal dioecy. This sexual system completely prevents autogamy but facilitates both geitonogamy and xenogamy. Geitonogamy occurs due to pollen transfer from the pollen of staminate phase flowers to the stigmatic lobes of pistillate phase mature buds within the plant; if pollen transfer occurs between flowers of different plants within or across populations, it results in xenogamy. The hairy-papillate stigmatic lobes in all the three species standing out distinctly from the mature buds were found to capture pollen driven by the wind. The powdery and multi-porate nature of pollen grains enable them to fly and disperse easily by wind and their dispersal is further propelled by vast uniform mats of populations of *Suaeda* species. The wind-driven pollen deposition on the stigmatic lobes and leaves can be seen with the naked eye and hence anemophily was considered to be effective. Anemophily was very effective

in high salt marshes devoid of water-logged conditions. In the low salt marshes where water-logged or water-saturated conditions occur, water currents were found to carry and disperse pollen effectively; here considerable aerial parts of the plants were merged or intermittently exposed and hence pollen was wet, making anemophily mostly ineffective. In all the three species, fruit set in open-pollinations is 93–95 % indicating the success rate of both geitonogamy and xenogamy; this high success rate could be due to the production of a single ovule in the flowers for which the deposition of a few viable pollen grains on the stigmatic lobes is sufficient.

Foraging activity and pollination

In all the three species, the flowers were foraged by bees, wasps and flies during daytime from 08:00–17:00 h with more foraging activity during 09:00–12:00 h and less activity during the afternoon period in high salt marshes and in low salt marshes where soil was not saturated with water (Tables 1, 3, 5; Figs. 1, 2, 4). The foraging activity pattern of all these categories of insects was almost similar and coincided well with the standing crop of floral rewards. *S. maritima* was foraged by *Nomia* bees (Image 4a) and one unidentified bee for pollen and nectar; by wasps, *Eumenes petiolata* (Image 4c), *Ropalidia* sp. (Image 4d), *Rhynchium* sp. and three unidentified wasp species (Image 4e–g), and by flies *Helophilus* sp. and *Sarcophaga* sp. (Image 4h) for nectar only. *Camponotus* ants also foraged for nectar (Image 4b), but they were resident foragers and remained on the plants throughout the flowering season. *S. monoica* was foraged by honey bees, *Apis dorsata* (Image 9a), *A. cerana* and *A. florea* for both pollen and nectar (Image 9b); by wasps, *Eumenes*

Table 1. List of insect foragers on *Suaeda maritima*

Order	Family	Genus	Species	Common name	Forage sought
Hymenoptera	Halictidae	*Nomia*	sp.	Alkali Bee	Pollen + Nectar
		Bee (Unidentified)	-	-	Pollen + Nectar
	Eumenidae	*Eumenes*	*petiolata* F.	Potter Wasp	Nectar
		Ropalidia	sp.	Paper Wasp	Nectar
	Vespidae	*Rhynchium*	sp.	Potter Wasp	Nectar
		Wasp (unidentified)	-	-	Nectar
		Wasp (unidentified)	-	-	Nectar
		Wasp (unidentified)	-	-	Nectar
	Syrphidae	*Helophilus*	sp.	Hover Fly	Nectar
	Sarcophagidae	*Sarcophaga*	sp.	Flesh Fly	Nectar
	Formicidae	*Camponotus*	sp.	Carpenter Ant	Nectar
Lepidoptera	Nymphalidae	*Danaus*	*chrysippus* L.	Plain Tiger	Leaf/dry fruited inflorescences sap
		Danaus	*genutia* Cr.	Striped Tiger	Leaf/dry fruited inflorescences sap
	Hesperiidae	*Borbo*	*cinnara* Wallace	Rice Swift	Leaf/dry fruited inflorescences sap
Coleoptera	Curculionidae	*Chrysochoris*	sp.	Beetle	Pollen

petiolata, *Rhynchium* sp. (Image 9c) and by the fly, *Sarcophaga* sp for only nectar (Image 9d). *S. nudiflora* was visited by *Nomia* bees for both pollen and nectar (Image 13a) while *Rhynchium* wasps for nectar only (Image 13b). In all the three species, thrips were nectar and pollen feeders (Image 13c); they collected most of the nectar during the mature bud stage and after anthesis, and also pollen during post-anthesis stage as soon as the anthers dehisce. Further, the iridescent green tortoise beetle, *Chrysochoris* (Scuteleridae) collected *S. maritima* pollen voraciously (Image 5d) while an unidentified immature stage of an insect was found to feed on the nectar and pollen of *S. nudiflora* (Image 13d). The percentage of foraging visits made by each category of insects varied with each *Suaeda* species. In *S. maritima*, bees made 21%, wasps 62% and flies 17% of the total foraging visits (Fig. 3). In *S. monoica*, bees made 54%, wasps 35% and flies 11% of the total foraging visits (Fig. 5). In *S. nudiflora*, *Nomia* bee made 48% and *Rhynchium* wasp made 52% of the total foraging visits.

In all the three plant species, the flowers with dehisced anthers representing the staminate phase attracted bees due to the clear-cut display of bright yellow pollen; the bees while collecting pollen and nectar from such flowers invariably also contacted accidentally the flowers in the pistillate phase occurring in the same cluster or nearby clusters on the same flowering branch due to their close proximity to each other and this foraging behavior was considered to be effecting geitonogamy. The production
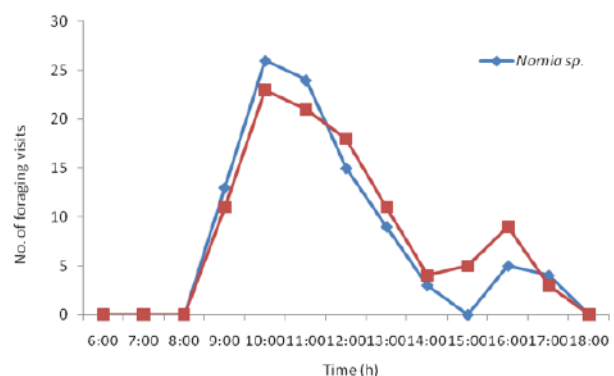

Figure 1. Hourly foraging activity of *Nomia* bee and *Rhynchiun* wasp on *Suaeda nudiflora*

of a few staminate phase flowers each day at the branch or plant level was found to be driving the bees to make frequent inter-plant visits within and between populations in the entire area in order to collect more nectar and pollen. They were effective carriers of pollen and their body washings revealed the presence of 142–156 pollen grains in case of *S. maritima* (Table 2), 195–219 pollen grains in case of *S. monoica* (Table 4), and 142 pollen grains in case of *S. nudiflora* (Table 6). Wasps, flies and ants attempted to collect nectar from pistillate and staminate phase flowers without any discrimination; such a foraging behavior was considered to be facilitating both geitonogamy and xenogamy. The flowers with minute traces of nectar were found to be driving the wasps to

Image 4. *Suaeda maritima*: a - *Nomia* sp. collecting pollen; b - *Camponotus* sp. collecting nectar; c - *Eumenes petiolata* collecting nectar; d - *Ropalidia* sp. collecting nectar; e–g - Unidentified wasps; h - *Sarcophaga* sp. (fly) collecting nectar. © A.J. Solomon Raju.

Table 2. Pollen recorded in the body washings of insects on *Suaeda maritima*

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Nomia sp.	10	78–206	142.4	36.81
Bee (unidentified)	10	93–227	156.5	41.58
Eumenes petiolata	10	25–113	81.7	26.92
Ropalidia sp.	10	36–75	55.2	12.61
Rhynchium sp.	10	45–87	68.3	14.91
Wasp (unidentified)	10	26–74	52.5	16.72
Wasp (unidentified)	10	43–91	64.4	15.53
Wasp (unidentified)	10	16–52	36.1	11.49
Helophilus sp.	10	20–64	45.3	12.80
Sarcophaga sp.	10	24–58	41.1	10.80
Camponotus sp.	10	32–84	50.7	16.45

Table 3. List of insect foragers on *Suaeda monoica*

Order / Family	Genus	Species	Common name	Forage sought
Hymenoptera Apidae	*Apis*	*dorsata* F.	Rock Honey Bee	Pollen + Nectar
	Apis	*cerana* F.	Indian Honey Bee	Pollen + Nectar
	Apis	*florea* F.	Dwarf Honey Bee	Pollen + Nectar
Eumenidae	*Eumenes*	*petiolata* F.	Potter Wasp	Nectar
Sarcophagidae	*Sarcophaga*	sp.	Flesh Fly	Nectar

make frequent inter-plant visits in order to collect more or optimal levels of nectar due to their high energy requirement. They were found to carry 36–82 pollen grains on their bodies in case of *S. maritima* (Table 2), 78 pollen grains in case of *S. monoica* (Table 4), and 61 pollen grains in case of *S. nudiflora* (Table 6) indicating their pollen carrying capacity. In case of flies, they tended to remain on the same plant for a long time collecting nectar from as many flowers as possible due to their low energy requirement. Their body washings revealed the presence of an average of 41–45 pollen grains in case of *S. maritima* (Table 2), 46 pollen grains in case of *S. monoica* (Table 4) and hence they were also pollen carriers to some extent. Ants as resident foragers and with a low energy requirement were considered to be important for geitonogamy if they were confined to the same plant and for xenogamy if they crawled to other nearby plants for nectar collection. They were found to carry an average of 50 pollen grains due to their nectar foraging activity. The nectar and pollen feeding activity of thrips was found to be an important driver, especially for bees and wasps to forage a number of individual flowers within and between populations. Certain of the insects recorded
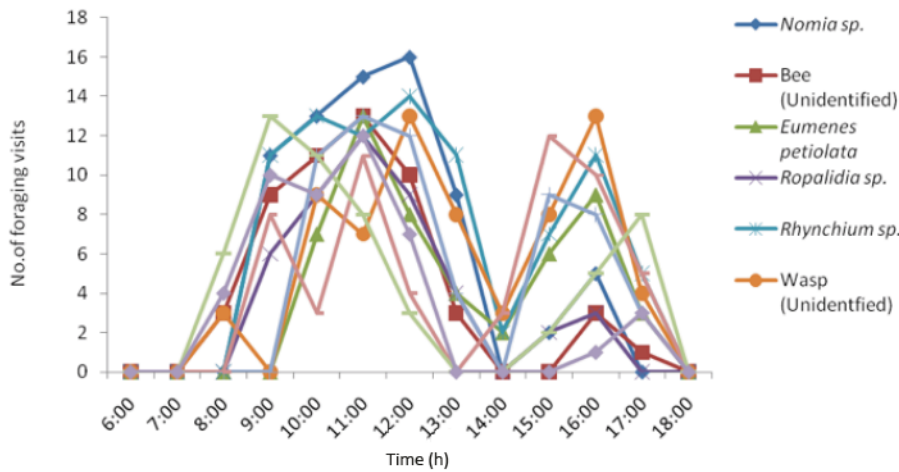
Figure 2. Hourly foraging activity of bees, wasps and flies on *Suaeda maritima*
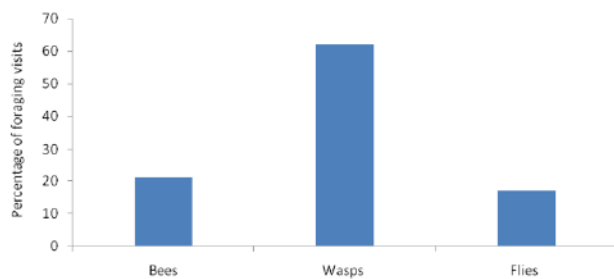

Figure 3. Foraging activity of bees, wasps and flies on *Suaeda maritima*

Table 4. Pollen recorded in the body washings of insects on *Suaeda monoica*

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Apis dorsata	10	128–263	195.1	44.04
Apis cerana	10	154–235	203.3	28.25
Apis florea	10	135–276	219.2	39.55
Eumenes petiolata	10	46–115	78.3	19.84
Sarcophaga sp.	10	31–73	46.4	12.74
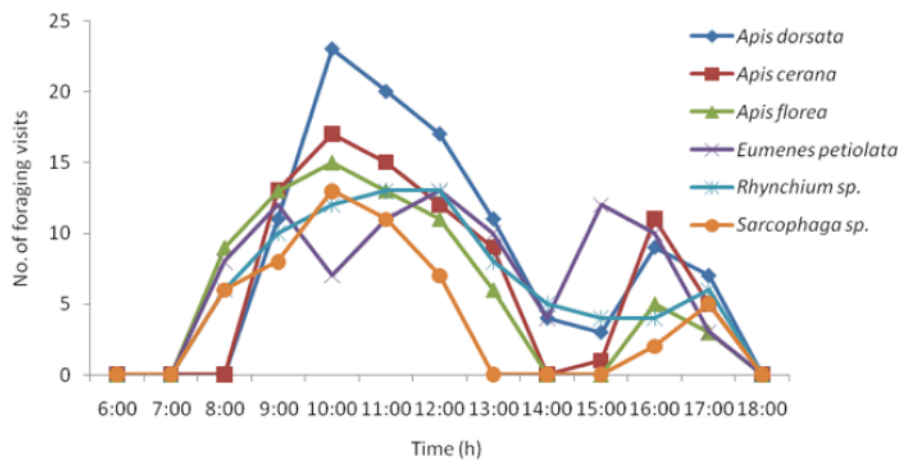
Figure 4. Hourly foraging activity of bees, wasps and flies on *Suaeda monoica*

were common to all the three plant species which co-exist in the same area and their alternate foraging visits could lead to the deposition of mixed pollen on each of these plant species. Such mixed pollen deposition could block the receptive area of the stigma lobes and reduce the opportunities for legitimate geitonogamous and xenogamous pollinations in each plant species.

In all the three *Suaeda* species, the nymphalid butterflies, *Danaus genutia* (Images 5a, 14a-c), *D. chrysippus* (Images 5b, 14d), the lycaenid *Euchrysops cnejus* (Image 14e), and the hesperiid, *Borbo cinnara* (Image 5c) were found to feed on the sap of leaves prior to flowering and on dry fruited branches. These butterflies mainly concentrated on *S. maritima* and *S. monoica* for sap collection. Further, they never visited the flowers for nectar collection and hence were not pollinators.

Image 5. *Suaeda maritima*: a - *Danaus genutia* collecting leaf sap; b - *Danaus chrysippus* collecting the sap from dry fruited inflorescence; c - *Borbo cinnara* collecting leaf sap; d - *Chrysocoris* sp. feeding on the pollen. © A.J. Solomon Raju.

Table 5. List of insect foragers on *Suaeda nudiflora*

Order / Family	Genus	Species	Common name	Forage sought
Hymenoptera Halictidae	*Nomia*	sp.	Alkali Bee	Pollen + Nectar
Vespidae	*Rhynchium*	sp.	Black Potter Wasp	Nectar
Lepidoptera Nymphalidae	*Danaus*	*chrysippus* L.	Plain Tiger	Leaf/dry fruited inflorescences sap
	Danaus	*genutia* Cr.	Striped Tiger	Leaf/dry fruited inflorescences sap
Lycaenidae	*Euchrysops*	*cnejus* F.	Gram Blue	Leaf/dry fruited inflorescences sap

Fruiting behaviour

In all the three species, fruit is an urticle with a 1.5mm wide and 1mm long persistent perianth (Image 3h). Hooded perianth segments cover seeds over the margins. It matures within 3–4 weeks (Image 6, 10a,b, 11e,f). Each fruit invariably produces a single seed. The seeds ripen from August–October. The seeds are brownish-black, smooth, glossy, ovoid, 1.2–1.5 mm diameter, finely punctate near the edges and beaked (Images 3i, 8j,k, 12i). The whole plant breaks off easily and rolls on the floor while shedding its diaspores. Fruits with seeds intact and/or seeds shed from fruits float on water due to their ability for buoyancy. The fruits and seeds thus disperse and settle in the entire extent of salt marshes or coastal areas.
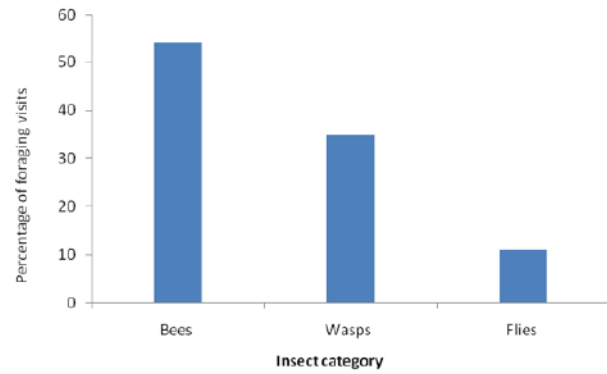

Figure 5. Percentage of foraging visits of different categories of insects on *Suaeda monoica*

Table 6. Pollen recorded in the body washings of insects on *Suaeda nudiflora*

Insect species	Sample size (N)	Number of pollen grains Range Mean S.D		
Nomia sp.	10	74–213	142.6	43.36
Rhynchium sp.	10	35–92	60.9	15.08

DISCUSSION

All the three *Suaeda* species are obligate succulent halophytes and grow well in high and salt marshes in different zonations of mangroves. Their growth within the interiors of mangroves is an excellent indicator of their tolerance level to high salinity. However, their growth rates vary depending on the locality, high or low salt marshes. The plants growing in high marshes are taller and profusely branched than those growing in low marshes. Wetson et al. (2012) reported such plasticity in plant growth pattern in *S. maritima* growing in the upper and lower salt marshes. Further, these authors also reported that plants growing at the extreme tide mark in the absence of other speciesgrow taller with many lateral branches. Ferren & Schenk (2003) reported two varieties, *richii* and *maritima* in *S. maritima* based on growth habit and seed size. Chapman (1947) also reported three principal varieties, *vulgaris, macrocarpa* and *flexilis* based on growth habit and seed size. Redondo-Gomez et al. (2008) reported that several *Suaeda* species exhibit seed dimorphism and produce both brown and black seeds simultaneously and these varying colorations reflect two different dormancy and germination strategies for survival in saline habitats. Ponnamperuma (1984) explained that occurrence of different growth forms

Image 6. *Suaeda maritima*: Different stages of fruiting. © A.J. Solomon Raju.

Image 7. *Suaeda monoica*: a. Individual plant, b. & c. Flowering inflorescences, d. Flower. © A.J. Solomon Raju.

Image 8. *Suaeda monoica*: a–d - Different stages of anthesis; e - Pollen grain; f & g - Trifid stigma; h & i - Ovule; j & k - Seed. © A.J. Solomon Raju.

reflect different soil conditions present in high and low salt marshes due to difference in aeration levels. The high salt marshes are well-drained and infrequently inundated by tidal water and hence have stable and good soil aeration due to rapid exchange between air and soil whereas the low salt marshes with water-logged conditions experience reduced availability of oxygen due to very slow diffusion of gases in water than in air. Further, the exchange of gases would fluctuate in both high and low salt marshes at different times due to variation in the frequency of submergence and quantum of tidal water causing inundation. As a result, the plants growing in the high and low salt marshes show different responses due to variation in soil aeration levels. All the three *Suaeda* species in this study did not show seed dimorphism either in size or in color suggesting that the variations in seed morphological characters could be situational depending on the nutrient and water levels, temperature, and other ecological factors present at the time of production of seeds in both annual and perennial *Suaeda* species.

Image 9. *Suaeda monoica*:
a - *Apis dorsata* feeding on pollen;
b - *Apis florea* feeding on pollen;
c - *Rhynchium* sp. collecting nectar;
d - *Sarcophaga* sp. collecting nectar.
© A.J. Solomon Raju.

Image10. *Suaeda monoica*: a. & b. Fruited inflorescences.
© A.J. Solomon Raju.

Khan & Weber (2003) reported that in annuals there is only one reproductive event in a lifetime, and this necessitates the ability to produce seeds with dormancy characteristics; when the seeds reach maturity, the environmental conditions may not be favorable for seedling growth and so germination is postponed until conditions are again more favourable. On the contrary, perennials reproduce by seed on multiple occasions, which means that producing genetic variations is not so paramount as it is with annuals; they may reproduce clonally, seeking to reproduce only the most successful genotype. However, as a long-term strategy, they may need to introduce new genetic individuals as and when conditions allow. In the present study, *S. maritima* and *S. monoica* are annuals and produce seeds once in their life with dormancy characteristics because their seeds germinate with a pause of 5–6 months from seed dispersal to seed germination. In these plants, genetic variation through sexual mode is very essential in order to withstand adverse soil conditions and produce stable populations. *S. nudiflora* is a perennial and produces seeds more than once in its life time and hence production of genetic variation is not very important for the production of stable populations. However, introduction of new genetic individuals as and when conditions allow is inevitable if this species is to survive and continuously produce stable populations in inhospitable habitats.

Abeywickrama & Arulgnanam (1993) described certain floral sex characters in *S. maritima* and *S. nudiflora*. Their descriptions indicate that these two species produce male flowers with a small ovary and female flowers with stamens reduced or absent; the styles vary from 2 to 3. These authors also mentioned that in *S. monoica*, each flower cluster consists of a large male flower with a rudimentary ovary surrounded by smaller female flowers with or without staminodes. Further, certain individual plants produce only female flowers. The present study contradicts these descriptions because all the three *Suaeda* species produce only bisexual flowers without styles; *S. maritima* and *S. monoica* flowers produce three sessile stigmas while *S. nudiflora* produces two sessile stigmas. Further, the inflorescences are characteristically axillary in *S. maritima* and *S. monoica* while they are borne both in the axils and terminally in *S. nudiflora*. The clustered cymes produce a varying number of flowers with each *Suaeda* species; they are 9–18 in *S. maritima*, 5–8 in *S. monoica* and 2–4 in *S. nudiflora*.

Rea (1969) & Kubitzki et al. (1993) reported that polygamy occurs in many species of Chenopodiaceae. Gynomonoecy in combination with protandry or protogyny occurs in some species. Kubitzki et al. (1993) stated that in this family, the presence of inconspicuous, minute, frequently perianth-less and mostly nectar-less flowers have been considered as adaptations for anemophily. These authors also mentioned that typical features of anemophily such as dusting pollen, waving, limp-filaments or simultaneous flower opening are usually required in order to be uniformly anemophilous. Zandonella (1977) noted that a switch-over from entomophily to anemophily or the reverse might have occurred in this family. Dalby (1962) stated that self-pollination also frequently occurs in various genera; one such genus is *Salicornia* in which the ripe dehiscing anthers stay in contact with the presumably receptive stigmas and in effect, selfing occurs. Kubitzki et al. (1993) felt that probably various degrees of balance between anemophily and self-pollination can be found in the members of this family. Dem'yanova (1977) reported that *S. microphylla, S. physophora, S. acuminata* and *S. linifolia*

Image 11. *Suaeda nudiflora*:
a - Individual plant;
b - Vegetative phase;
c- Flowering phase;
d - Flowering inflorescence;
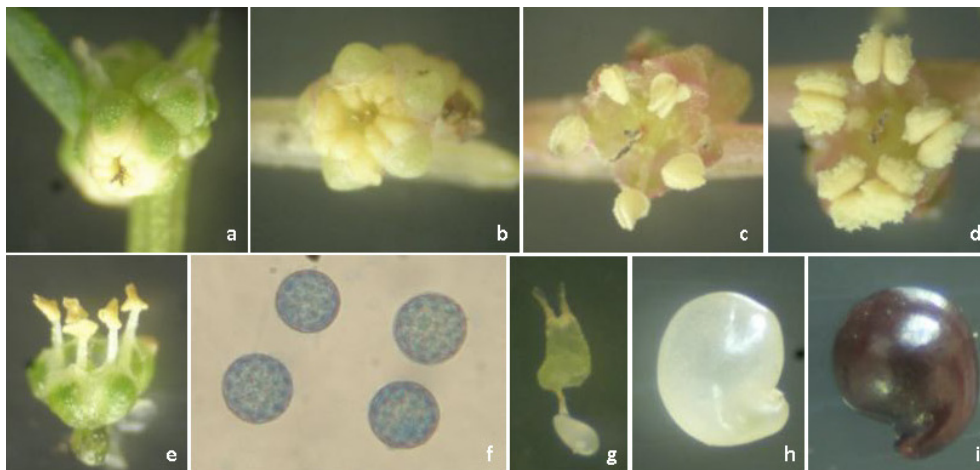e&f - Fruited inflorescences.
© A.J. Solomon Raju.

Image 12. *Suaeda nudiflora*:
a–d - Different stages
of anthesis; e - Flower
showing the position of
stamens; f - Pollen grains;
g & h - Ovule; i - Seed.
© A.J. Solomon Raju.

are predominantly anemophilous; entomophily also exists but it has no significant importance. The flowers receive visits of *Halictus* bees during the staminate phase by which time the stigma begins to wither and does not accept pollen. Keighery (1979) reported that honey bees and syrphid flies collect pollen from the flowers of *Suaeda australis* but this author did not state whether they are pollinators or not. Chapman (1947) mentioned that *S. maritima* flowers are homogamous or feebly protandrous; autonomous autogamy is easily possible. The flowers are nectar-less and hence insect activity is absent. Bassett & Crompton (2011) recorded that *S. maritima* is wind-pollinated. Naskar & Mandal (1999) reported that *S. maritima* is pollinated by wind, water currents and flies.

In the present study, all the three *Suaeda* species are nectariferous and offer nectar in minute to trace amounts. The flowers are dichogamous with strong protogyny; they are pistillate during the mature bud stage and staminate after anthesis, the situation of which completely prevents autonomous or facilitated selfing within the flower. This sexual system is almost typical of temporal dioecy. Cruden & Hermann-Parker (1977) coined the term 'temporal dioecism" to describe the pattern of sexual alternation within the individual plants to facilitate outcrossing through the promotion of xenogamy. The sexual system functional in *Suaeda* species is a type of temporal dioecy. In these species, the strong dichogamy appears to have evolved to promote outcrossing, however, both pistillate and staminate phase flowers are available at any given point within the individual plants
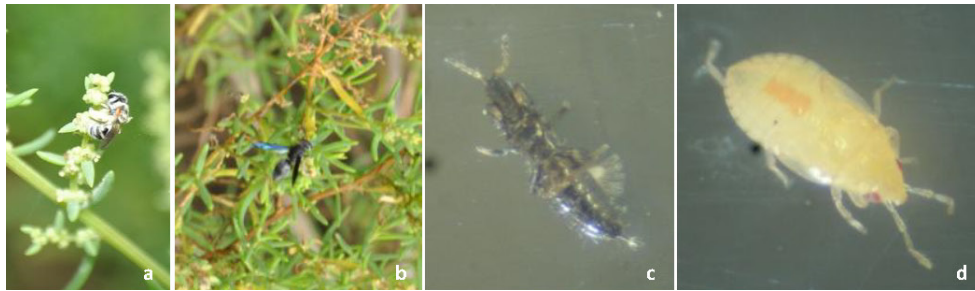
Image 13. *Suaeda nudiflora*:
a - *Nomia* sp. collecting
pollen; b - *Rhynchium* sp.
collecting nectar; c - Thrips,
d - Unidentified insect.
© A.J. Solomon Raju.

Image 14. *Suaeda nudiflora*: Sap collection from leaves:
a–c - *Danaus genutia*; d - *Danaus chrysippus;* e - *Euchrysops cnejus*.
© A.J. Solomon Raju.

facilitating the occurrence of geitonogamy. Therefore, *Suaeda* species seem to have evolved temporal dioecy to promote outcrossing through xenogamy while keeping the option open for selfing through geitonogamy. The fruit set recorded in open-pollinations substantiates the functionality of such a sexual system. This sexual system is essential for these species to produce seeds in isolated individuals in news areas in order to build up their populations.

Renner & Feil (1993) stated the plants that possess morphological traits fulfilling the aerodynamic requirements of pollen dispersal and capture favor the evolution of anemophily. Wind pollination might evolve when pollinators are scarce, absent or deliver poor quality pollen when plants colonize areas with low insect abundance (Weller et al. 1998; Gomez & Zamora 1996). Anemophilous plants do not invest in resources that attract pollinators, such as showy flowers, nectar and scent. Instead, they produce a large quantity of light, dry pollen from small, plain flowers that can be carried by wind. Female structures are adapted to capture the passing pollen from the air but the majority of pollen goes waste. Niklas (1985) stated that plants with small, colorless, odorless and nectar-less flowers, reduced or no perianth, projecting exserted stamens away from the boundary layer of main flower to higher wind speeds, production of large quantity of light, dry and dusty pollen, permitting the unobstructed removal of pollen, and well exposed large, hairy and feathery stigma to capture pollen are adapted for anemophily. In all the three *Suaeda* species, the flowers have a combination of anemophilous and entomophilous traits. The anemophilous traits are odorless, unattractive flowers with inconspicuous perianth, the exserted stamens projected out of the perianth and light, dry and dusty pollen while entomophilous traits are production of nectar, dorsi-fixed stamens, production of a moderate quantity of pollen, and promiscuity of flower for nectar and pollen collection for insects. Field observations indicated that anemophily is effective especially in high salt marshes due to the occurrence of moderate to high wind speeds in the mangrove areas; the pollen deposition by wind on the stigmas can be easily recorded and the leaves also get coated with pollen despite their succulent nature. Insects pollinate the flowers while collecting the forage from pistillate and staminate phase flowers. Bees visit only staminate flowers due to the availability of both nectar and pollen; while approaching these flowers they effect either geitonogamy or xenogamy accidentally because of the clustered form of flowers. Wasps, flies and ants probe pistillate phase mature buds and staminate phase flowers of the concerned plant species indiscriminately, but the pistillate phase flowers are non-rewarding while the staminate phase flowers are rewarding. As a result, these insects effect geitonogamy and xenogamy. *Chrysocoris* beetle is a voracious pollen feeder and deprives the flowers of pollen in *S. maritima*; its pollen feeding activity indirectly compels the bees to collect pollen from different plants and such a foraging behavior results in the promotion of xenogamy. Further, thrips in all the three species and one insect in an

immature stage in the case of *S. nudiflora* deplete both nectar and pollen being available considerably and such a state of floral rewards drive all the insect species, except ants to make frequent inter-plant visits within the species and across *Suaeda* species; this leads to the promotion of outcrossing through xenogamy. The occurrence of these species in the same area and their simultaneous flowering facilitates the insects to deposit mixed pollen consisting of the pollen of all the three species on their stigmas and this pollen discounting diminishes outcross siring success. In this context, it is to be stated that insect activity is not very intense on these plant species, it is prominent on *S. maritima* and *S. monoica* while it is not so in *S. nudiflora* due to the production of very inconspicuous flowers when compared to the other two species. Pollen discounting did not show any affect on seed set rate and it is reflected in the very high fruit set rate in open-pollinations. This could be because of the requirement of a few viable pollen grains for stigmas to produce a single seed per flower. Further, water currents also disperse pollen and pollinate flowers within and between plants of all the three species in inundated or submerged localities. In these localities, anemophily or entomophily is not very effective due to the wet state of pollen or flowers or even plants. Therefore, these three *Suaeda* species use a combination of pollination by wind, insects and water currents simultaneously. The function of three pollination syndromes in these plant species gives them flexibility to maximize fruit or seed set rate through outcrossing as well as selfing through geitonogamy (Culley et al. 2002).

Ridley (1930) noted that Chenopodiaceous seeds are dispersed by wind, water and animals. Chapman (1947) stated that in *S. maritima*, seed germination occurs from March onwards and fruits disperse from October onwards. Fruit dispersal occurs by tides and they can float for three days and then settle in the soil. In the present study also, it is found that in all the three *Suaeda* species, the whole plant breaks off and rolls on the floor while shedding its diaspores. Fruits with seeds intact and/or seeds shed from fruits float on water due to their ability for buoyancy. The fruits and seeds thus disperse, settle in the entire extent of salt marshes or coastal areas and germinate in the mid-summer season when salinity is very high in high and low salt marshes.

Jones & Blum (1983) reported that the pyrrolizidine alkaloids play a key role in host-plant selection and as a sex pheromone in certain danaid butterflies. These butterflies apply from their proboscides a fluid capable of dissolving alkaloids and then re-imbibe it. Both sexes of these butterflies store alkaloids apparently for defense (Edgar et al. 1976; 1979; Rothschild et al. 1979;

Conner et al. 1981). Owen (1971) reported that danaine butterflies use withered and damaged plants and floral nectar as sources of alkaloids. *D. chrysippus* uses the pyrrolizidine alkaloids to protect itself from its predators and synthesizes the courtship pheromone; maternal and parental contributions of alkaloids play an important role to protect the most vulnerable stage, the egg (Meinwald 1990). This butterfly species and also *D. plexippus* when equipped with these alkaloids have been experimentally proved to be unpalatable to their predators by Edgar et al. (1976). Boppre (1983) reported that *Tirumala petiverana* collects sap from *Heliotropium pectinatum* in East Africa. Mathew & Anto (2007) reported that *T. limniace* uses the pyrrolizidine alkaloids to deter its predators, the garden lizards. In the present study, the nymphalid butterflies, *Danaus genutia, D. chrysippus*, the lycaenid *Euchrysops cnejus*, and the hesperiid, *Borbo cinnara* have been found to collect sap from the leaves before flowering and dry fruiting branches of all the three *Suaeda* species. The presence of alkaloids, triterpenoids, sterols and various other chemicals have been reported in *S. maritima, S. monoica* and *S. nudiflora* (Al-Mohammadi et al. 2005; Suganthy et al. 2009; Gurudeeban et al. 2011; Ravikumar et al. 2011; Satyavani et al. 2012). Therefore, *Suaeda* species studied now appear to be an important source of alkaloids for all the recorded butterfly species and the latter use them to deter their predators.

The genus *Suaeda* has both C_3 and C_4 photosynthetic pathways with both the categories of species commonly growing side by side; C_4 species are mostly annuals in central Asia (Glagoleva et al. 1990). C_4 pathway is an adaptive mechanism to grow in stressful environments; these species grow abundantly in drier and more saline sites and persist throughout the dry season due to their succulence (Fisher et al. 1997). *S. maritima* is a C_3 species with austrobassioid leaf anatomy and colonizes all areas where perennial species are absent due to sensitivity to competitive interactions (Yeo & Flowers 1980; Andres 1989). *S. monoica* and *S. nudiflora* are C_4 species and grow abundantly in hot, dry, high-light saline environments (Shomer-Ilan et al. 1975; Ehleringer & Monson 1993; Singh et al. 2004; Patel & Pandey 2009). In the present study, *S. maritima* and *S. monoica* are annuals while *S. nudiflora* is a perennial; all the three grow side by side in both high and low salt marshes. *S. nudiflora* is dominant particularly in drier, saline areas; its successful growth in such areas could be related to the C_4 photosynthetic pathway. Further, *S. maritima* and *S. monoica* have been found to grow mostly in areas where *S. nudiflora* does not grow. Such a growth pattern appears to be related to sensitivity of the first two species to competitive interactions arising

from the perennial species, *S. nudiflora* which is usually available throughout the year and displays extensive mat-forming growth. Nevertheless, C_4 species, *S. monoica* and *S. nudiflora* can be successfully used for eco-restoration in saline areas where other species do not grow.

Manousaki & Kalogerakis (2011) reported that halophytes are more efficient in withstanding and adapting themselves to several abiotic factors due to their several inherent basic biochemical tolerance mechanisms when compared to glycophytic plants. They are naturally better adapted to cope with environmental stresses including heavy metals compared to salt-sensitive crop plants commonly chosen for phytoremediation purposes for the removal of heavy metals from soils. They are potentially ideal plants for phyto-extraction or phyto-stabilization applications of heavy metal polluted soils and moreover of heavy metal polluted soils affected by salinity. Some salt-excreting halophytes use their excretion mechanism in order to remove the excess of toxic metal ions from their sensitive tissues and hence act as biological pumps for heavy metals. Phyto-desalination has attracted much interest for the desalination of soils with the use of salt-accumulating halophytes which receive and accumulate high concentrations of salt in their aboveground tissues and consequently the saline soils can be improved by harvesting the plants. Cherian & Reddy (2003) stated that salinity is a major problem in irrigated agriculture especially in the arid and semiarid environments. While glycophytes undergo growth inhibition in saline environments either due to a decline in water uptake caused by the increase in external osmotic pressure or due to ionic imbalance in the cytosol, halophytes evolved mechanisms for controlled influx of sodium and chloride ions to be used for their benefit in a saline environment. Reddy et al. (2010) reported that halophytes are widely used due to their high economic values like fodder, oil, fuel and so forth, and also for ecological interests like soil desalination, dune fixation, phyto-remediation, landscaping and ornamental purpose. A further domestication of halophytes as potential crop plants for biomass production is an emerging field towards rehabilitation of salinized lands in semi-arid and arid areas. Soils adjacent to the coastal areas under irrigation or otherwise get enriched with various materials including hazardous elements from the discharges of industrial effluents, which in turn pose a great problem for the reclamation of soils and for their use in cultivation. Manousaki & Kalogerakis (2011) reported that *S. maritima* accumulates high concentrations of salt in its aboveground tissues, and consequently, saline soils can be upgraded by harvesting the plants on a regular basis.

Ravindran et al. (2007) also reported that *S. maritima* accumulates high concentrations of salts in its tissues and reduces salts in the saline land to a great extent. These authors called it a salt accumulating halophyte and can be used successfully to accumulate salt in highly salinized areas for crop production after a few repeated cultivations and harvests. Reddy et al. (2010) also mentioned that *S. nudiflora* accumulates and sustains the salinity levels to nearby double that of seawater. It could be cultivated for its economic importance even on highly polluted soils for reclamation. Further, it is also used as a source of biological salt or oil. Singh et al. (2004) reported that the seeds of *S. nudiflora* contain approximately 30-35% oil and hence has the potential as a future oil seed crop. It is highly suitable for producing high protein biomass in saline soils with its C_4 photosynthetic pathway. Therefore, the studied *Suaeda* species can be used to extract salt, desalinate saline soils and use such soils for normal plantation or cultivation. Salinization is a serious problem confronting sustainable agriculture in irrigated production systems in semi-arid and arid regions where plant growth is directly affected by high levels of sodium chloride and other salts (Marschner 1986). In India, about 30 million ha of coastal land is still barren and uncultivable because of bad soil affected by salinity (Singh & Surendra 1994). In this context, it is quite appropriate to consider the *Suaeda* species as potential desalinating agents for highly saline soils in order to convert bad soils into fertile soils for crop production. Further, they can also be used for the clean-up of polluted soils through phyto-remediation programs.

REFERENCES

Abeywickrama, B.A. & P. Arulgnanam (1993). The Coastal Plants of Sri Lanka, Part I (Salt Marsh Plants). UNESCO: Man and the Biosphere National Committee for Sri Lanka. Publication No. 20. Natural Resources, Energy and Science Authority of Sri Lanka. Colombo, 19p.

Al-Mohammadi, S.S., E. Al-Khateeb & S. Al-shamma (2005). Phytochemical investigation of *Suaeda baccata* (Chenopodiaceae). *Al-Mustansiriyah Journal for Pharmaceutical Sciences* 2: 51–57.

Andres, I.M. (1989). Anatomia foliar en plantas de saladares mediterraneos costeros. Dicotiledoneas. *Candollea* 44: 435–452.

Bassett, I.J. & C.W. Crompton (2011). The genus *Chenopodium* in Canada. *Canadian Journal of Botany* 60: 586–610; http://dx.doi.org/10.1139/b82-080

Chapman, V.J. (1947). *Suaeda maritima* (L.) Dum. *Journal of Ecology* 35: 293-302.

Cherian, S. & M.P. Reddy (2003). Evaluation of NaCl tolerance in the callus cultures of *Suaeda nudiflora* Moq. *Biologia Plantarum* 46: 193–198; http://dx.doi.org/10.1023/A:1022838224429

Conner, W.E., T. Eisner, R.K.V. Meer, A. Guerrer, D. Ghitingelli & J. Meinwald (1981). Precopulatory sexual interaction in an Arctiid Moth (*Utetheisa ornatrix*): Role of a pheromone derived from dietary alkaloids. *Behavioural Ecology & Sociobiology* 9: 227–235.

Cruden, R.W. (1977). Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.

Cruden, R.W. & S. Herrmann-Parker (1977). Temporal dioecism: an alternative to dioecism? *Evolution* 31: 863–866.

Culley, T.M., S.G. Wellder & A.K. Sakai (2002). The evolution of wind pollination in angiosperms. *Trends in Ecology and Evolution* 17: 361–369; http://dx.doi.org/10.1016/S0169-5347(02)02600-9

Dafni, A., P.G. Kevan & B.C. Husband (2005). *Practical Pollination Biology*. Enviroquest Ltd., Ontario, 583pp.

Dalby, D.H. (1962). Chromosome number, morphology and breeding behavior in the British Salicornieae. *Watsonia* 5: 150–162.

Dem'yanova, E.I. (1977). Flowering and pollination ecology of some species of Suaeda of southeast Kazakh, USSR. *Biologicheskie Nauki (Moscow)* 20: 91–96.

Edgar, J.A., M. Boppre & D. Schneider (1979). Pyrrolizidine alkaloid storage in African and Australian danaid butterflies. *Experientia* 35: 1447–1448.

Edgar, J.A., P.A. Cockrum & J.L. Frahn (1976). Pyrrolizidine alkaloids in *Danaus plexippus* L. and *Danaus chrysippus* L. *Experientia (Basel)* 32: 1535–1537.

Ehleringer, J.R. & R.K. Monson (1993). Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology, Evolution and Systematics* 24: 411–439; http://dx.doi.org/10.1146/annurev.es.24.110193. 002211

Ferren, W.R. Jr. & H.J. Schenk (2003). *Suaeda* Forsskal ex J.F. Gmelin., pp. 390–398. In: *Flora of North America, North of Mexico*. Eds. FNA Editorial Committee, Vol. 4. Magnoliophyta: Caryophyllidae, Part I, Oxford University Press, New York.

Fisher, D.D., H.J. Schenk, J.A. Thorsch & W.R. Ferren Jr. (1997). Leaf anatomy and subgeneric affiliations of C_3 and C_4 of *Suaeda* (Chenopodiaceae) in North America. *American Journal of Botany* 84: 1198–1210.

Flowers, T.J., P.F. Troke & A.R. Yeo (1977). The mechanism of salt tolerance in halophytes. *Annual Review of Plant Physiology* 28: 89–121; http://dx.doi.org/10.1146/annurev.pp.28.060177.000513

Gelin, Z., S.L. Mosyakin & S.E. Clemants (2003). Chenopodiaceae. *Flora of China* 5: 351–414.

Glagoleva, T.A., E.V. Voznesenskaya, K.G. Kol'chevskii, N.I. Kocharya, M.V. Pakhomova, M.V. Chulanovskaya & Y.V. Gamaley (1990). Structural-functional characteristics of halophytes of the Ararat Valley. *Soviet Plant Physiology* 37: 822–829.

Gomez, J.M. & R. Zamora (1996). Wind pollination in high-mountain populations of *Hormathophylla spinosa* (Cruciferae). *American Journal of Botany* 83: 580–585.

Gurudeeban, S., T. Ramanathan, K. Satyavani & T. Dhinesh (2011). Standardization of DNA isolation and PCR protocol for RAPD analysis of *Suaeda* sp. *Asian Journal of Biotechnology* 3: 486–492; http://dx.doi.org/10.3923/ajbkr.2011.486.492

Jones, T.H. & M.S. Blum (1983). Arthropod alkaloids: distribution, functions and chemistry, pp. 34–84. In: Pelletier, S.W. (ed.). *Alkaloids: Chemical and Biological Perspectives*, Wiley, New York.

Keighery, G.J. (1979). Insect pollination of *Suaeda australis* (Chenopodiaeae). *Western Australian Naturalist* 14: 154.

Khan, M.A. & D.J. Weber (eds.) (2003). *Ecophysiology of High Salinity Tolerant Plants.* Springer, Netherlands, 399pp.

Kubitzki, K., J.G. Rohwer & V. Bittrich (1993). *Flowering plants - Dicotyledons: Magnoliid, Hamamelid and Caryophyllid Families (The Families and genera of Vascular Plants).* Springer Science & Business Media, 653pp.

Manousaki, E. & N. Kalogerakis (2011). Halophytes present new opportunities in phytoremediation of heavy metals and saline soils. *Industrial & Engineering Chemistry Research* 50: 656–660.

Marschner, H. (1986). *Mineral Nutrition of Higher Plants.* Academic Press, London, 674pp.

Mathew, G. & M. Anto (2007). In situ conservation of butterflies through establishment of butterfly gardens: A case study at Peechi, Kerala, India. *Current Science* 93: 337–347.

Meinwald, J. (1990). Alkaloids and isoprenoids as defensive and signaling agents among insects. *Pure & Applied Chemistry* 62: 1325-1328.

Naskar, K. & R. Mandal (1999). *Ecology and Biodiversity of Indian Mangroves*. Daya Publishing House, New Delhi, 754pp.

Niklas, K.J. (1985). The aerodynamics of wind-pollination. *Botanical Review* 51: 328–386.

Owen, D.F. (1971). *Tropical Butterflies*. Clarendon Press, Oxford, 214pp.

Patel, N.T. & A.N. Pandey (2009). Effect of soil salinity on growth, water status and nutrient accumulation in seedlings of *Suaeda nudiflora* (Chenopodiaceae). *Anales de Biologia* 31: 61–70.

Ponnamperuma, F.N. (1984). Effects of flooding on soils, pp. 9–45. In: Kozlowski, T.T. (ed.). *Flooding and Plant Growth*. Academic Press, New York.

Ravikumar, S., M. Gnanadesigan, S.J. Inbaneson & A. Kalairasi (2011). Hepatoprotective and antioxidant properties of *Suaeda maritima* (L.) Dumort ethanolic extract on concanavalin - A induced hepatotoxicity in rats. *Indian Journal of Experimental Biology* 49: 455–460.

Ravindran, K.C., K. Venkatesa, V. Balakrishnan, K.P. Chellappan & T. Balasubramanian (2007). Restoration of saline land by halophytes for Indian soils. *Soil Biology & Biochemistry* 39: 2661–2664; http://dx.doi.org/10.1016/j.soilbio.2007.02.005

Rea, J. (1969). Biologia floral de la quinua (ch. Quinoa). *Turrialba* 19: 91–96.

Reddy, M.S., M.P. Joshi, S.P. Dave, S. Adimurthy, V.S. Susarla, A.S. Mehta, P.V.S. Rao, M.P. Reddy & G. Ramachandraiah (2010). Bromide tolerance in plants: a case study on halophytes of Indian coast. *SRX Ecology* 2010: 1–6; http://dx.doi.org/10.3814/2010/650678

Redondo-Gomez, S., E. Mateos-Naranjo, J. Cambrolle, T. Luque, M.E. Figueroa & A.J. Davy (2008). Carry-over of differential salt tolerance in plants grown from dimorphic seeds of *Suaeda splendens*. *Annals of Botany* 102: 103–112; http://dx.doi.org/10.1093/aob/mcn069

Renner, S.S. & J.P. Feil (1993). Pollination of tropical dioecious angiosperms. *American Journal of Botany* 80: 1100–1107.

Ridley, H.N. (1930). *The Dispersal of Plants Throughout The World.* Reeve & Co., Ashford, Kent, 744pp.

Rothschild, M., R.T. Alpin, P.A. Cockrum, J.A. Edgar & P. Fairweather (1979). Pyrrolizidine alkaloids in Arctiid moths (Lepidoptera) with a discussion on host plant relationships and the role of these secondary plant substances in the Arctiidae. *Biological Journal of Linnean Society* 12: 305–326.

Satyavani, K., S. Gurudeeban, T. Ramanathan & T. Balasubramanian (2012). Toxicity study of silver nanoparticles synthesized from *Suaeda monoica* on Hep-2 cell line. *Avicenna Journal of Medical Biotechnology* 4: 35–38.

Shomer-Ilan, A., S. Beer & Y. Waisel (1975). *Suaeda monoica*, a C_4 plant without typical bundle sheaths. *Plant Physiology* 56: 676–679; http://dx.doi.org/10.1104/pp.56.5.676

Singh, R.P. & S. Surendra (1994). *Sustainable Development of the Indian Arid Zone: A Research Perspective.* Vedams Books Ltd., New Delhi, 335pp.

Singh, A., J. Chikara & J.B. Pandya (2004). Plant regeneration from callus cultures in *Suaeda nudiflora* (Willd.) Moq. *Indian Journal of Biotechnology* 3: 454–456.

Suganthy, N., S.K. Pandian & K.P. Devi (2009). Cholinesterase inhibitory effects of *Rhizophora lamarckii, Avicennia officinalis, Sesuvium portulacastrum* and *Suaeda monoica*: mangroves inhabiting an Indian coastal area (Vellar estuary). *Journal of Enzyme Inhibition and Medicinal Chemistry* 24: 702–707; http://dx.doi.org/10.1080/14756360802334719

Weller, S.G., A.K. Sakai, A.E. Ranki, A. Golonka, B. Kutcher & K.E. Ashby (1998). Dioecy and the evolution of pollination systems in *Schiedea* and *Alsinidendron* (Caryophyllaceae: Alsinoideae) in the Hawaiian Islands. *American Journal of Botany* 85: 1377–1388.

Wetson, A.M., C. Zorb, E.A. John & T.J. Flowers (2012). High phenotypic plasticity of Suaeda maritima observed under hypoxic conditions in relation to its physiological basis. *Annals of Botany* 109: 1027–1036; http://dx.doi.org/ 10.1093/aob/mcs014

Yeo, A.R. & T.J. Flowers (1980). Salt tolerance in the halophyte, *Suaeda maritima* L. Dum.: evaluation of the effect of salinity upon growth. *Journal of Experimental Biology* 31: 1171–1183.

Zandonella, P. (1977). Morphologie pollinique et mode des pollinisation. *Pollen et Spores* 19: 119–142.