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Reproductive ecology of the dioecious and chamaechorous littoral spinegrass, *Spinifex littoreus* (Burm.f.) Merr. (Poaceae)

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Abstract

Spinifex littoreus is an essential constituent of coastal sand dune ecosystem. It forms separate colonies of male and pistillate plants characterizing dioecious sexual system. The flowering occurs during October-January but within this period, male plants begin flowering two weeks early to pistillate plants. The florets are born in inflorescence, each consisting of several spikelets which vary in number between male and pistillate spikelets. Further, individual spikelets of male plants produce several florets while those of pistillate plants produce characteristically a single floret. In pistillate florets, the anthers are rudimentary, indehiscent and sterile while female sex is perfectly functional. The stamens and stigmas positioned at the apex of the florets are completely exposed, the position of which facilitating pollen flow from male plants to pistillate plants with pollination as an end result. Anemophily is the rule in this plant as insect foraging activity is completely absent which is attributed to lack of floret attraction, lack of nectar and low nutrition value of pollen. Fruit set did not exceed 16% which is attributed to low nutrient availability and alkaline sandy soils. Chamaedorea is the mode of fruit dispersal and it is applicable only to Infructescence of pistillate plants. Infructescence buried by sand germinate and produce new plants. The plant also propagates through vegetative mode through stolon formation. It is an effective sand binder, stabilizes the sand dune and hence is useful in coastal green belt development.

Keywords: Spinifex littoreus, dioecy, anemophily, infructescence, chamaedorea, stoloniferous

1. Introduction

Spinifex is a genus of perennial coastal plants and most common in sand dunes along the coasts of Africa, Middle East, Asia, Australia, New Zealand and New Caledonia. The species of this genus aid in the stabilization of the sand and form an important part of the entire sand dune ecosystem^[1]. The genus is characterized by a stellate inflorescence made of radiating racemes that resemble the shape of a sea urchin ^[2]. In this genus, S. sericeus and S. littoreus have been reported by many authors with reference to their taxonomy and floral aspects ^[3]. S. littoreus is distributed on coastal sand dunes throughout Southeast Asia, including Japan, China, Taiwan, Indonesia and India^[4]. The sand dunes provide a highly stressful environment for plants ^[5] which commonly face excess light, drought stress, toxic ion concentrations, strong winds, and low nutrient availability ^{[5,} ^{6]}. S. littoreus has certain adaptive traits such as leaf tissue succulence and accumulation of solutes in order to grow, survive and invade sand dunes ^[7]. Leaf tissue succulence allows the plants to maintain the physiological functions under drought^[8]. S. littoreus is reported as dioecious species distributed along the coast of Bengal [9], in the Indian subcontinent [10-14]. But it is reported it as androdioecious in Malaysia [15], tropical Southeast Asia [16], Java [17], and Ashmore Reef, Timor Sea ^[18]. Based on herbarium specimens used from most of these places for S. littoreus, Connor ^[2] reported that it is dioecious in its continental distribution but hermaphrodites are present on oceanic islands; the occurrence of hermaphroditism is reported as breakdown of dioecy here. Further, he also noted that this species is anemophilous. In India, S. littoreus has not been studied for its reproductive ecology despite its common occurrence along the coastal sand dunes of both east and west coasts and its importance as efficient sand binder stabilizing the dunes and maintaining their topography with little alteration especially during windy seasons, and in aiding the coast protection from sand erosion. Therefore, the intent of the present study is to provide information on the reproductive ecology of *S. littoreus*, which is the main constituent of sand dune vegetation growing along Visakhapatnam-Bheemili coast line in the State of Andhra Pradesh, India.

2. Materials and Methods

Wild populations of Spinifex littoreus growing as widespread colonies in the sand dune ecosystem along the shoreline of the Bay of Bengal near Rushikonda (Lat. 17°46'57.07°N and Long. 83°23'6.41°E) in Visakhapatnam Rural Mandal of Visakhapatnam District of Andhra Pradesh, India, were selected for study during June 2017-February 2019. This plant grows as separate colonies, each colony representing either male or pistillate plants. Observations regarding the organization of inflorescences, the spatial positioning of flowers, and their position on the plant were made since these features are regarded as important for achieving pollination. The flower longevity was recorded by marking twenty just open flowers and following them until fall off. Anthesis was initially recorded by observing ten marked mature buds of male and pistillate florets in the field. Later, the observations were repeated five times on different days, each day observing ten marked mature buds in order to provide accurate anthesis schedule for both plant sexes. The same marked mature buds on male plants 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 sex, shape, size, colour, odour, sepals, petals, stamens and ovary were described for each floret sex.

Twenty-five mature but un-dehisced anthers from male florets were collected from five randomly chosen plants and placed in a Petri dish. Later, each time a single anther was taken out and placed on a clean microscope slide (75 x 25 mm) and dabbed with a needle in a drop of lactophenolaniline-blue. The anther tissue was then observed under the microscope for pollen, 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 and per floret was determined. The characteristics of pollen grains were also recorded. The stigma receptivity was observed by H₂O₂ test as given in Dafni *et al.* ^[19]. The male and pistillate plants were never visited by any insect species during their flowering period and hence observations on insect activity could not be made. The study area is windy consistently with variation in speed through the day and night. The pollen transport from staminate plants was observed visually and it was quite prominent from late morning to early afternoon because of high light, high temperature and low humidity.

In pistillate plants, fruit maturation period and seed dispersal and establishment were observed in the field. For natural fruit set rate, 985 spikelets of pistillate plants were tagged and followed for six months for calculating fruit set rate. Further, field observations were carefully made on vegetative propagation involving stolon formation and subsequent detachment from the parent plant.

3. Results

The Plant, flowering and floral morphology

It is a prominent coastal perennial and stoloniferous colonyforming grass with strong creeping stolon-forming stems. Individual plants root and branch copiously at nodes. Each node produces adventitious roots and upright, silvery and hairy green leaves; eventually a discrete plant is formed and becomes independent if there is sufficient space (Figure 2af). Leaf blades are in-rolled, curved, rigid, pungent, usually 5-12 mm wide and 36-42 cm long with spiny apex and densely ciliate ligule. The plant is dioecious producing male and pistillate florets on different individuals. Both male and pistillate plants form separate colonies of almost equal size in the same open sand dune areas (Figure 1a,b). The flowering begins in October (Figure 1c) and ceases in January (Figure 1d) but male plants flower early to pistillate plants by about 2 weeks. The male and pistillate plants grow as separate colonies in the same area and this situation is quite prominent during flowering phase as their inflorescence morphology is different for each sex. Flowering shoots ascend to 30-80 cm and produce stellate inflorescence comprising a terminal main inflorescence with subjacent lateral racemes, each subtended by a spatheole and embraced at base by subtending leaf. In male plants, the inflorescence is a raceme bearing 10-18 sessile spikelets and terminates with a short bristle (Figure 3a-d). Each spikelet

consists of two glumes and produces 6.42 ± 1.08 green sessile and pungent florets which are 9.6 ± 2.3 mm long and 11.8 ± 5.0 mm diameter. The florets are arranged in two-tier system, upper and lower ones at each point. Each floret has a pair of membranous lodicules which represent reduced perianth, one palea and one lemma; the last one larger than the palea. Both palea and lemma surround and protect the fertile pollen iferous anthers of the florets. The stamens are three and each stamen is 6. 2 ± 0.6 mm long; the filament is liguliform and tipped with 5.2 ± 0.7 mm long, shortly tailed anthers. In each floret, all anthers protrude beyond the lemma and stand exposed. In pistillate plants, the inflorescence is a raceme with 5-7 sessile spikelets, each consists of two glumes and produces a solitary, sessile, green, pungent 9.6 \pm 2.3 mm long floret. Each floret has a pair of membranous lodicules, one palea and one lemma. The last two enclose the functional fully developed gynoecium with 14.6 ± 0.9 mm unilocular ovary with a single ovule and 9.8 ± 0.7 mm long stigma and styles and delicate rudimentary stamens which consist of delicate liguliform filaments and white pollen-less anthers. The stamens are three, rudimentary, sterile, indehiscent and positioned atop of the floret; they often remain entrapped in stigmas. The styles are two, each tipped with a plumose stigma and positioned at the apex of the floret. In pistillate plants, the rudimentary stamens and the plumose stigmas positioned outside the top of the floret are clearly visible.

Floral biology

In both male and pistillate plants, florets open during 0500-0900 h with many opening during 0600-0700 h (Figure 4ac). In both floret sexes, the lemma and palea slightly separate and display the sex organs; anthers are flexible, quite prominent and displayed at the apex of male florets while the styles and stigma are long and displayed along with rudimentary stamens at the apex of the pistillate florets. In male florets, anthers dehisce during flower-opening by longitudinal slits and pollen is presented along the line of dehiscence (Figure 3e-g). In a floret, two anthers dehisce during flower-opening while the remaining anthers dehisce any time later in the day. The pollen grains are pale yellow, powdery, 41. 085 \pm 5.69 µm; they are 3,432.1 \pm 417.86 per anther and $10,296.3 \pm 1,307.17$ per floret. The male florets last for 4 days. In pistillate florets, the rudimentary anthers are indehiscent and inconspicuous (Figure 4h) while the plumose stigmas are quite prominent, receptive after floweropening which is indicated by the slight separation of lemma and palea and remain so until the evening of the next day (Figure 4g,i).

Pollination

Male florets act as pollen donors while pistillate florets as recipients of pollen. The florets of these two sexes are not attractive and never visited by any insect species during the entire duration of flowering season. As the anthers are positioned at the apex of the male florets, the powdery pollen is driven away easily by winds prevailing along the coastline. Further, the colonies of sexes of both plants occur in open areas in sand dunes, wind facilitates pollen flow with great ease from male plants to pistillate plants. The oscillating plumose stigmas at the tip of pistillate florets capture the wind-driven pollen easily and in effect pollination occurs (Figure 4d-f). The open areas where the plant formed colonies of male and pistillate plants facilitate International Journal of Botany Studies

the occurrence of anemophily even with moderate wind speed. The florets of both sexes were never visited by any insect species during the flowering season, although honey bees and stingless bees were found in the habitat. These bees were found visiting the flowers of *Ipomoea pes-caprae* (L.) R.Br. (Convolvulaceae) which is growing as small patches here and there in the area.

Fruiting ecology

In pistillate plants, the florets upon pollination and fertilization develop into 1-seeded (5 mm long) caryopsis of 9.5 ± 0.7 mm in which the ovary wall is united with the seed coat (Figure 5b-e). The fruit is tipped with withered stigma

and rudimentary anthers (Figure 5a). Natural fruit set rate is 16% only. It is equal to seed set rate as each pistillate floret produces only one ovule. The stellate inflorescence with several 1-floreted racemes produce a single terminal head which matures within 4-5 weeks. The seed-head is globose, spiny at the tip and detaches as wind balls from the plant. These wind balls aided by spines roll along the ground by wind, also get buried due to sand blasting and even transported by sea water. Field observations indicated that seeds covered by moving sand germinate and produce new plants. Further, the plants continue to grow despite being buried by moving sand from time to time and is an efficient sand binder, forming large colonies and stabilizing dunes.



Fig 1: Spinifex littoreus : a. Male populations, b. Pistillate plant populations, c. Flowering phase, d. Flowering cessation phase.



Fig 2: Spinifex littoreus - Vegetative propagation: a-e. Stages of stoloniferous rooting at the nodes, f. Trailing of stoloniferous rooting.

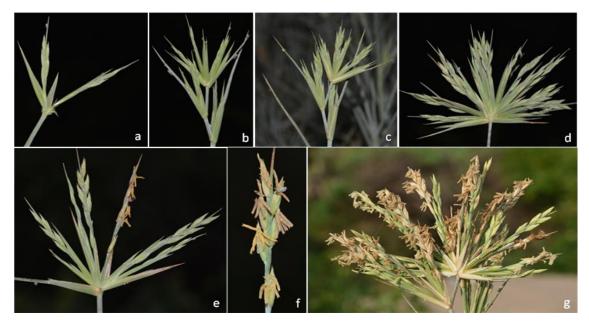


Fig 3: Spinifex littoreus - Male plant: a-d. Stages of maturation of spike inflorescence; e-g. Flowering spikes with dehisced anthers

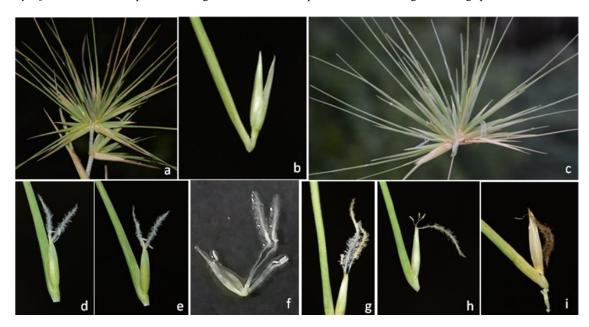


Fig 4: Spinifex littoreus - Pistillate spike inflorescence: a. & b. Mature buds, c. Anthesis flower, d-f. Swinging receptive plumose stigmas according to wind speed and direction, g. Stigmas showing signs of receptivity loss by withering, h. Flower showing three rudimentary indehiscent anthers lacking pollen (staminodes), i. Flower with completely withered stigma.



Fig 5: Spinifex littoreus: a. Maturing fruit tipped with withered stigma and rudimentary anthers, b. & c. Matured fruit, d. & e. Seeds.

4. Discussion

In the coastal areas, the fore-shore zone region is usually occupied by the hermaphroditic species, *Ipomoea pes-caprae*. This plant with long creeping branches forms extensive mats and stabilizes the sand dunes. Another important effective sand binder is *Spinifex littoreus* which

grows well in the fore-shore zone. This species with its long rhizomes spreads horizontally on the sand and branches out long roots which go obliquely below the sand to considerable depth ^[20]. In the study area, the sand dune represent open habitat with almost no vegetation. The only species that occurs in this area is *Ipomoea pes-caprae* which

has small colony-like populations here and there. S. littoreus with creeping stoloniferous stems formed colonies invasively in open habitats but is not associated with I. pescaprae. The open habitats of fore-shore zone region is characterized by salt spray, drought, high light, high temperature and strong winds and shifting sand. But, S. littoreus withstands this hostile environment and grows well and sexual reproduction. using asexual Asexual reproduction involves production of new plants and this mode is functional through formation of strong stolons on the soil surface and each stolon grows as clone of the parental plant at the end of it. The stolons develop into new independent plant when severed from the parent plant. Sexual reproduction involves seed production from pollinated and fertilized pistillate florets/plants. Seeds germinate and produce new plants. Therefore, the dual modes of reproduction enables S. littoreus to spread as an invasive species, especially in open sand dunes.

Dioecism is relatively a rare sexual system among the grasses and reported in about twenty genera only. In Poaceae, it is most common in Ailuropodinae and Chlorideae tribes of Poaceae^[21]. Further, this sexual system is known only in the Old World genera, Spinifex and Zygochloa of the tribe Paniceae. These genera are psammophilous but the former is coastal while the latter is inland in distribution. Further, he also noted that male and female plants of *Spinifex* form colonies of equal size ^[3]. S. littoreus distributed in western Java, on Moluccan Islands and in the Philippines, display trimonoecious sexual system. In this species, the same individual produces two types of 2flowered spikelets. One spikelet consists of lower male floret with three polliniferous anthers and lacking gynoecium completely and upper hermaphrodite floret with three polliniferous anthers and style and stigma; this spikelet represents and romonoecism. The second spikelet consists of lower floret with three sterile anthers and upper floret with a gynoecism and three male sterile anthers ^[2]. The production of two types of spikelets by the same plant in S. littoreus represents a trimonoecious inflorescence [22]. The andromonoecious spiklets either alone or mixed together with female flowers on the same plant in S. littoreus appear to have evolved to increase the chances of pollination and seed set that were reduced by the large spatial extent of single sex colonies and the over dispersal of male and female plants ^[2]. In this study, S. littoreus produces male and pistillate plants as separate colonies of almost equal size in the open sand dune areas providing ample opportunities for pollen flow from staminate to pistillate florets. The flowering is partially asynchronous as male plants flower about two weeks early to pistillate plants. The inflorescence is a raceme with several spikelets but their number is more in male plants than in pistillate plants. Further, each spikelet consists of several florets which are arranged as upper and lower ones at each point in male plants while it is a solitary floret in each spikelet in pistillate plants. The anthers are fertile in male florets while they are sterile in female florets but in the latter, gynoecium is functional. The rudimentary stamens in pistillate florets of S. littoreus indicate that the plant is actually a hermaphroditic but the circumstantial selection pressures might have favoured the evolution of dioecism by the suppression of function of male sex in a set of individuals characterizing pistillate florets and total elimination of female sex in another set of individuals characterizing male florets and these two sets of individuals

eventually began to form separate colonies in the same area. Dioecism is an evolved sexual system that completely prevents the occurrence of selfing and favours only outcrossing. Further, this sexual system would reduce the risks of high levels of geitonogamous anemophily in very large hermaphrodite colonies of long-lived plants ^[23]. In this context, it is not unreasonable to mention the statement of Connor ^[3] that restoration of fertility in *Spinifex* species would involve one step from filamented rudimentary, bilobed, small, pollenless anthers to polliniferous ones. Harlans ^[24] stated this step is a "genetic call" of the presumed ancestral condition and would probably require no more than a dominant gene. Therefore, S. littoreus appears to have the inherent flexible character of switching from hermaphroditism to dioecism retaining the opposite sex organ in rudimentary form and from dioecism to hermaphroditism by activating the function of suppressed sex organ in each floret sex depending on the circumstantial selection pressures, and hence, in general dioecism in Spinifex seems to be unstable.

Faegri and van der Pijl^[25] stated that anemophilous plants produce small flowers with highly reduced perianth parts and lacking nectaries or if present, they are non-functional. Linder [26] and Friendman and Barrett [27] stated that anemophilous plants display the traits such as small, unisexual flowers with dry pollen that facilitates its dispersal by wind. Moore ^[28] reported that features of anemophilous pollination syndrome include a lack of scent production, a lack of showy floral parts resulting in inconspicuous flowers, reduced production of nectar, and the production of enormous pollen. Shukla et al. ^[29] mentioned that anemophilous pollen grains are light and non-sticky, so that they can be transported by air currents. Ackerman^[30] reported that anemophilous plants produce flowers with well-exposed stamens to enable the pollen for dispersal by wind currents and large and feathery stigma to trap airborne pollen grains easily. Further, their pollen tends to be smaller and lighter than pollen from entomophilous ones, with very low nutritional value to insects. Dowding [31] stated that wind-pollinated flowers usually produce only single ovules because of the small chance of multiple pollen grains landing on each stigma. Linder ^[26] reported that wind-pollinated plants transport pollen as single units because the chance of capturing each pollen grains is an independent event. In consequence, the plants that evolved anemophily show a reduction in ovule number in line with the dispersal of pollen as single units. In this study, it is found that S. littoreus flowers display anemophilous traits as mentioned above by different authors. The male and pistillate florets are inconspicuous with reduced perianth, lack of scent and nectary. In male florets, the anthers are completely exposed, produce ample pollen at inflorescence level and disperse as single units by wind due to their light, powdery, non-sticky and dry nature. In pistillate florets, the ovary has only one ovule and the styles and stigmas are completed exposed at the apex. All these traits displayed by both male and pistillate florets of S. littoreus are perfect adaptations for anemophily and are in conformity with the floral traits mentioned above, which are described by different authors. The exposure of anthers at the apex of male florets facilitate dispersal of pollen easily by air currents, and the exposure of feathery stigmas at the apex of pistillate florets facilitate to capture the airborne pollen easily and in effect pollination is ensured ^[32]. The day-time anthesis of florets is an additional advantage for the promotion of anemophily. Further, the colonies of both sexes occur in open habitats in sand dunes that receive moderate to high wind speeds. This habitat is quite conducive for the aerodynamic requirements for anemophily indicating that open habitats and anemophily evolve in a dependent way and are associated positively [31]. Anemophily in this species is an adaptation that helps to separate the male and female reproductive systems of a single plant, reducing the effects of inbreeding ^[30]. The total absence of insect foraging activity on S. littoreus could be because of lack of floral attraction, lack of nectar and low nutrient value of pollen. Despite favourable wind environment, S. littoreus is able produce 16% fruit set and such a low fruit set rate could be attributable to low nutrient availability and alkaline sandy soils [5].

The present study found that the pistillate plants of S. littoreus produces aggregate fruits which are called Infructescence within a month or so. The globose Infructescence blow along the sand as wind balls and most of them finally settle among its own colonies while some others are covered my moving sand. The stiff spines at the tip of fruits appear to be promoting fruit dispersal and aiding in anchoring of the Infructescence in sand. This form of dispersal of Infructescence characterizes Chamaedorea. Infructescence burial by sand appear to be important to gather and accumulate moisture in order to provide conducive environment for the germination of seeds to produce new plants. The plant is deep-rooting, thrives in raw sand and is tolerant of salt spray, prolonged dryness, extreme temperatures, high intensity, and strong wind ^[6, 33]. The upright shoots aid in reducing surface wind velocity and accumulating sand with frequent burial of stems and leaves ^[6]. The plant stabilizes the sand dunes by holding the sand together with its roots and stolons, and hence forms an important constituent of the entire sand dune ecosystem^[1] and useful in coastal green belt development. Since the leaves are spiny and stiff, the animals do not feed on them ^[20]. However, it is reported that a plethora of birds, mammals and reptiles depend on the colonies of S. littoreus for their survival and is considered a keystone of its environment^[2].

In general, marine plants possess a wide spectrum of bioactive compounds which have commercial potential in pharmaceutical industry ^[34]. Because, as halophytes, they tolerate harsh saline and arid conditions by synthesizing a number of active chemicals to maximize their fitness and many such chemicals are sources of potent medicines against a number of chronic ailments ^[35]. *S. littoreus* as a halophyte growing well in sand dune ecosystem tolerates a highly stressful environment which is characterized by high temperature, high light, salt spray and soil salinity ^[5, 6]. In this context, it is suggested that *S. littoreus* is to investigated for its bioactive compounds in order to evaluate their potential in pharmaceutical industry.

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