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Sexual systems, pollination modes and fruiting ecology of three common herbaceous weeds, *Aerva lanata* (L.) Juss. Ex Schult., *Allmania nodiflora* (L.) R.Br. and *Pupalia lappacea* (L.) Juss. (Family Amaranthaceae: Sub-family Amaranthoideae)

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ABSTRACT

Aerva lanata and Pupalia lappacea are perennial herbs while *Allmania nodiflora* is an annual herb. *A. lanata* is dioecious with bisexual and female plants while *P. lappacea* and *A. nodiflora* are hermaphroditic. In *P. lappacea*, the flowers are borne as triads with one hermaphroditic fertile flower and two sterile flowers alternately along the entire length of racemose inflorescence. *A. lanata* and *A. nodiflora* flowers are nectariferous while *P. lappacea* flowers are nectarless. The hermaphroditic flowers of *A. lanata*, *A. nodiflora* and *P. lappacea* are homogamous and facilitate autonomous selfing as they are self-compatible and self-pollinating. In *A. lanata*, female flowers are apomictic. Pollination also occurs by gravity within the flower, by wind and insects in *A. lanata,* by wind, insects and rain water in *A. nodiflora* and by wind and bees in *P. lappacea*. In all the three species, autochory, anemochory and hydrochory are functional; additionally ombrochory and myrmecochory are functional in *A. nodiflora* and epizoochory and anthropochory in *P. lappacea*. Therefore, *A. lanata* with sexual and asexual modes, *A. nodiflora* and *P. lappacea* with only sexual mode, and all the three species with more than one pollination mode and seed dispersal mode are able to invade different habitats with varied environmental conditions and grow as widespread weeds in the tropics.

Keywords: *Aerva lanata, Allmania nodiflora, Pupalia lappacea*, dioecy, hermaphroditism, apomixis, autonomous selfing, anemophily, entomophily, ombrophily, autochory, anemochory, hydrochory, ombrochory, myrmecochory, epizoochory, anthropochory.

1. INTRODUCTION

The family Amaranthaceae comprises of herbs or shrubs, rarely lianas and small trees. The inflorescence is either axillary or terminal spiciform or capitate spike disposed sometimes in racemose or paniculate syninflorescences with individual small and inconspicuous flowers uniseriate perianth of five tepals, five stamens with dorsifixed and introrsely dehiscent anthers, a single style and a unilocular ovary formed from the union of two or three carpels; they are basically subtended by a ventral bract and two lateral bracteoles (Kapralov et al. 2012). In this family, plant species are speculated to be monoecious, dioecious and polygamous with bisexual or unisexual flowers (Anilkumar 2006). Allogamy by dichogamy is probably the norm in this family. In hermaphroditic flowers and species demonstrating monoecy, protogyny is the usual method to ensure cross-pollination. Dioecism is functional in *Amaranthus, Chamissoa, Deeringia, Iresine* and *Aerva javanica* while polygamy in *Aerva* species, *A. lanata, A. leucura* and *A. sanguinolenta* (Kapralov et al. 2012). In this family, the pollen with stellate pore ornamentation is unique in certain genera. In this pollen, the pore membrane bears wedge-shaped segments as flecks of ektexine or ektexinous bodies in a radial arrangement covering more or less equal area of the pore and distally elongated into an outwardly projecting hook (Livingstone et al. 1973; Skvarla and Nowicke 1976; Borsch 1998). The functional role of these hooks is to cling to insect pollinators or to the stigmatic surface. A thickened structure over each pore might be advantageous to taxa inhabiting xeric environments as it could help to prevent water loss (Livingstone et al. 1973) but Muller and Borsch (2005) stated it is not correct to correlate the presence of this structure over each pore on the pollen to xeric habitats because the plants growing in both xeric and semi-xeric habitats possess pollen with stellate pore ornamentation and hence it is associated with more specialized insect pollination syndromes. Townsend (1993) stated that information on the pollination biology of Amaranthaceae is scarce and completely lacking for the plant species with stellate pore ornamentation. Amaranthaceae members are speculated to be wind-pollinated but Muller and Borsch (2005) reported that many genera are in fact frequently visited by insects and vividly colored tepals with stellate pore ornamentation suggest insects as pollen vectors.

Khan et al. (1970) documented that *Aerva* genus has about 29 species distributed in Asia, Africa and Australia. Burkill (1985) reported that *Aerva* genus represents perennial herbs and under shrubs and distributed in the North Temperate zone, especially in the Mediterranean regions and Asia. About 20 species occur in Pakistan and India and most of them are used in traditional medicinal system. Thiv et al. (2006) reported that *Aerva* is native to the palaeotropics throughout continental Africa, Madagascar and smaller islands Rodrigues, Mauritius and Socotra, through parts of the Middle East, India, and southeast Asia. Different authors (Pullaiah 2006; Ahmed et al. 2010; Quattrocchi 2012) reported that *Aerva* genus is popular as medicinal herb in several traditional systems of medicine because the species of this genus are used as a valuable remedy for fever, rheumatism, gastric troubles, cough, sore throat, and wounds. Khan et al. (1970) reported that *A. javanica* is dioecious and in its entire distribution range is primarily obligate apomictic with female plants as common and male plants as rare. As an obligate apomictic, it produces seeds in the absence of pollen and probably displays genetic variation through mutation, auto-segregation and somatic crossover under varied environmental conditions. Since it is a dioecious weed, its long range dispersal is possible only if it is accompanied by apomictic mode of reproduction. *A. pseudotomentosa* is a hermaphroditic and its flowers display pollen and pollen germination on the pistil indicating that it is not an apomictic. Guha Bakshi (1984) reported that *A. lanata* as a common weed is distributed in India and also in Arabia, tropical Africa, Sri Lanka, Philippines and Java. Vetrichelvan and Jegadeesan (2002) reported that *A. lanata* is found in the tropical regions of Africa, India, Arabia and the Philippines. Gunatilake et al. (2012) reported that *A. lanata* is wide spread in the drier parts of the tropics and the sub tropics of the world. Kirtikar and Basu (1996) mentioned that *A. lanata* is abundant on the plains in the warmer parts of India and identified by its small bunches of woolly flowers that bloom on axillary branches. Different authors (Jawaweera 1981; Prasad et al. 1986; Rajesh et al. 2010) reported that *A. lanata* is used in the treatment of lithiasis, cough, asthma, and headache and as an antidote for rat poisoning. It is also used as a decoction or as an herbal tea without other herbs in Ayurveda system. Different authors noted the floral sex of this species differently. It is bisexual (Warrier 1994; Athira and Nair 2017) and often bisexual (Ranjan and Deokule 2013); it is normally self-pollinated (Saxena and Brahmam 1994; Athira and Nair 2017).

The genus *Allmania* is widely distributed in tropical Asia from India and Ceylon eastwards to Thailand, Malaya, South China, Indonesia and the Philippines. It represents three species, *A. nodiflora, A. pyramidalis* and *A. longipedunculata* which have been distinguished based mostly on leaf shape and peduncle length (Anilkumar 2006). Backer (1949) classified this genus into *A. nodiflora* with sessile heads and *A. pyramidalis* with peduncled ones. Raju and Padmavathi (1997) documented variations in the length of branch, size and texture of the leaf, color of the flower and size of the inflorescence in specimens collected from Andhra Pradesh. But, these variations change depending on the habitat conditions in different localities and hence are these characters are not useful for taxonomic studies and hence *Allmania* has been treated as a monotypic genus with a single species, *A. nodiflora*. Anilkumar

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(2006) provided certain floral characters such as the presence of five free tepals, staminal filaments united into a cup below, the absence of pseudo-staminodes, the presence of bilocular anthers, short style, bi-lobed stigmas, uni-ovulate ovary and utricle fruit with arillate seeds to distinguish the genus from other genera of the family. In *A. nodiflora*, the pollen characters such as spheroidal, tectate, tectum punctate or slightly anulopunctate with evenly distributed micro-spines and pores with the latter consisting of 5-14 closely adjoined ektexinous bodies arranged in a mosaic-like pattern indicate the least specialized *Deeringia*-type of pollen (Borsch 1998). Recently, Solomon Raju and Prasada Rao (2018) reported that *A. nodiflora* with greenish-white flower form is hermaphroditic, anemophilous and entomophilous. Fruit is a 1-seeded fruit and dehisces by circumscissile lid to dispersed the seed indicating the function of autochory; it is also anemo- and myrmecochorous. But, it is not known whether the yellow flower form of this species also shows the same structural and functional aspects of reproductive ecology.

Pupalia genus is listed in sub-tribe Aervinae of the tribe Amarantheae in Amaranthoideae subfamily (Townsend 1993) and consists of four species, *P. micrantha, P. grandiflora, P. robecchii* and *P. lappacea* with herbaceous or sub-shrub habit in the tropical or subtropical Old World from West Africa to Malaysia and the Philippines (Townsend 1985). In this genus, the inflorescence is terminal and each bract has a triad of single fertile flower with modified sterile flower on each side. The fertile flower produces five stamens fused at the extreme base forming a fleshy disc and 1-ovuled ovary (Townsend 1985). The modified sterile flowers form hooked spines alongside the fertile flowers and hooks grouped into clusters of 5-10 on short stalks on a common peduncle (Yang and Chen 2006). In this genus, the pollen has stellate pore ornamentation (Livingstone et al. 1973). The pollen is *Psilotrichum* type displays two morphologically allied types with Centemopsis type. It is nearly spheroidal, mesoporia protruding around the pores, tectate, tectum coarsely punctate, with one or two microspines positioned in the area of least distance between pores. The number of membrane bodies (hooks) varies between 6 and 10 in different plants (Borsch 1998). *P. lappacea* is widespread in the tropics and subtropics of the Old World and occurs from Arabia to India, Malaya, Indonesia, the Philippines and New Guinea in Asia. It is also found in Egypt and throughout tropical Africa to South Africa and Madagascar; but it is an introduced weed in Australia and elsewhere in the tropical world (CSIR 1950; Townsend 1985). In Amaranthaceae, the pollen is pantoporate and distinguished into fenestrate and periporate types. *P. lappacea* pollen is periporate type; its exine is metareticulate as the reticulum is composed of mesoporia and pores (Borsch and Barthlott 1998; Shinwati et al. 2004). *P. lappacea* is a minor source of pollen for honey bees (Onyango 2019). *P. lappacea* is widely used in folklore medicine. The leaf paste with edible oil is used to treat bone fractures and inflammatory conditions (Jalalpure et al. 2008). The fruit juice is used to treat cuts, mixed with palm oil to treat boils and applied to leprosy sores after making them bleed while the fruit soup is used for cough and fever. In Africa, fruit is used as an ingredient in enema preparation. Burnt plant is mixed with water to treat flatulence. It is also used to treat jaundice, abdominal colics, cephalgias, diarrheas, paralysis, erectile dysfunction, vomiting and malaria (Bero et al. 2009). None of Pupalia species have been investigated for their sexual reproduction and seed dispersal aspects thus despite their value in traditional medicine and widespread distribution in the tropical Old World.

As there is lack of information or general scarcity or speculative nature of information on the pollination biology of *Aerva lanata, Allmania nodiflora* (Yellow flower form) and *Pupalia leppacea*, the present study was contemplated to provide certain details of floral biology, pollination, fruiting and seed dispersal to understand their widespread distribution in the tropical world as successful weeds.

2. MATERIALS AND METHODS

Aerva lanata, Allmania nodiflora (Yellow flower form) and *Pupalia leppacea* growing in open habitats and wayside of Andhra University campus were used for study during January 2019 to December 2020. They form pure populations in open habitats and mixed populations in habitats inhabited by different seasonal herbaceous species that flourish during wet season. These species were investigated for plant phenology, flowering season, flower morphology, floral biology, sexual system, breeding system, foraging activity, pollination mechanism, pollinators, fruiting and seed dispersal aspects. All these aspects were carefully observed to record differences in these aspects between these three species. Stigma receptivity was tested using H_2O_2 test as prescribed in Dafni et al. (2005). A total of seventy inflorescences were tagged on different plants and followed for 2-4 weeks to record fruit development period and fruit and seed set rates. *In situ* observations were made on fruit dehiscence and seed dispersal and seed germination aspects to record the modes of seed dispersal and germination ability depending on soil moisture status.

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3. RESULTS

AERVA LANATA

Phenology and floral sex: It is a woody, erect to prostrate slightly succulent perennial herb with woody root system that grows in damp open habitats, waste and disturbed areas and waysides (Figure 1a). The stem is long and ascending with whitish to yellowish hair, sprawling and spread widely. Leaves are simple, shortly petiolate, alternate, densely tomentose, elliptic to lanceolate, cuneate at the base and rounded and apiculate at the apex. The plant appears throughout the year in damp habitats while it perishes in dry habitats. In damp habitats, vegetative growth, flowering and fruiting events occur continually but all these events are quite prolific during wet season (Figure 1b). The inflorescence is a sessile 6-14 mm long cylindrical spike with a few silky white to cream-colored closely crowded flowers, solitary and borne in the axils of leaves of main stem or of short axillary branches (Figure 1c). The spikes being white to cream in color are quite distinct again the green foliage and are well displayed because of the prostrate to erect nature of the stems and axillary branches. The floral sex indicates that individual plants are either bisexual or pistillate; the bisexual flowers are morphologically and functionally hermaphroditic while pistillate flowers are strictly female and hence they are referred to as female flowers.

Bisexual flowers: The flowers are minute, 2-3 mm long, sessile, greenish-white and actinomorphic (Figure 1d,e). Perianth is represented by five calycine membranous 1.5-2 mm long tepals which are woolly on the dorsal side. The stamens are five, fertile, alternating with five linear staminodes and united forming a cup at the base. The fertile stamens possess 1.5-1.7 mm long dorsifixed dithecous yellow incurved anthers which dehisce by longitudinal slits during mature bud stage. Each anther produces copious pollen. The pollen grains are yellow, spheroidal, pantoporate (8-12 apertures), isopolar, granulate and 13.5 ± 0.19 µm (Figure 1g). The pistil consists of a globose 1-1.5 mm long, bicarpellary, unilocular syncarpous ovary with one campylotropous funicular ovule arranged on basal placentation, short simple style with divergent scarcely papillose bifid stigma. The style and stigma are placed well below the height of stamens; the stigma is receptive during anthesis and remains so for a few hours.

Female flowers: The flowers are minute, 2.5-3.5 mm long, sessile, greenish-white and actinomorphic (Figure 2a-c). Perianth is represented by five calycine membranous 2.5-3 mm long tepals which are woolly on the dorsal side. The staminodes are ten without anthers but all are united forming a cup at the base. The pistil consists of a globose 2-2.5 mm long, bicarpellary, unilocular syncarpous ovary with one campylotropous funicular ovule arranged on basal placentation (Figure 2e), short simple style with well developed divergent scarcely papillose bifid stigma. The style and stigma are placed well above the height of staminodes (Figure 2d); the stigma is receptive during anthesis and remains so for a few hours.

Figure 1. *Aerva lanata*: a. Habit, b. Flowering individual, c. Inflorescence, d. & e. Anthesis stages of hermaphrodite flower, f. Position of stamens and stigma, g. Pollen grain.

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Pollination: In bisexual flowers, the place of stamens well above the stigma facilitates the occurrence of selfing as soon as the anther dehisce during or after anthesis by the falling of granular pollen on the stigma by gravity (Figure 1f). The pollen fall within the same flowers and pollen flow between flowers of the same and different plants are also driven by wind. In female flowers, the pollen was found to be deposited on the stigma of some flowers indicating that there is pollen flow between bisexual and female plants.

In both bisexual and female plants, the flowers are nectariferous with nectar secreted in traces which glitters against sunlight but it is quite clear in female flowers compared to bisexual ones. Thrips species, *Thrips hawaiiensis* and and *Frankliniella schultzei* (Thysanoptera: Thripidae) were found in buds of both bisexual and female flowers indicating that they use them for breeding and subsequently for feeding on pollen and nectar in bisexual flowers and on nectar in female flowers. These thrips became apparent during and after anthesis and moved between flowers of the same or different spikes of the same or different adjacent conspecific plant(s). They were resident foragers and visited both bisexual and female plants to collect forage and such a foraging activity was considered to be enabling pollen flow between bisexual flowers to result in self- or cross-pollination and between bisexual and female flowers to result in cross-pollination. Further, the stingless bee, *Trigona iridipennis* (Hymenoptera: Apidae) often collected pollen and/or nectar from bisexual flowers and nectar from female flowers; its foraging activity was considered to be instrumental in effecting either self- or cross-pollination in bisexual plants and cross-pollination in female plants. Despite the foraging activity of resident thrips and non-resident stingless bee, many stigmas in female plants were found to be without pollen deposition.

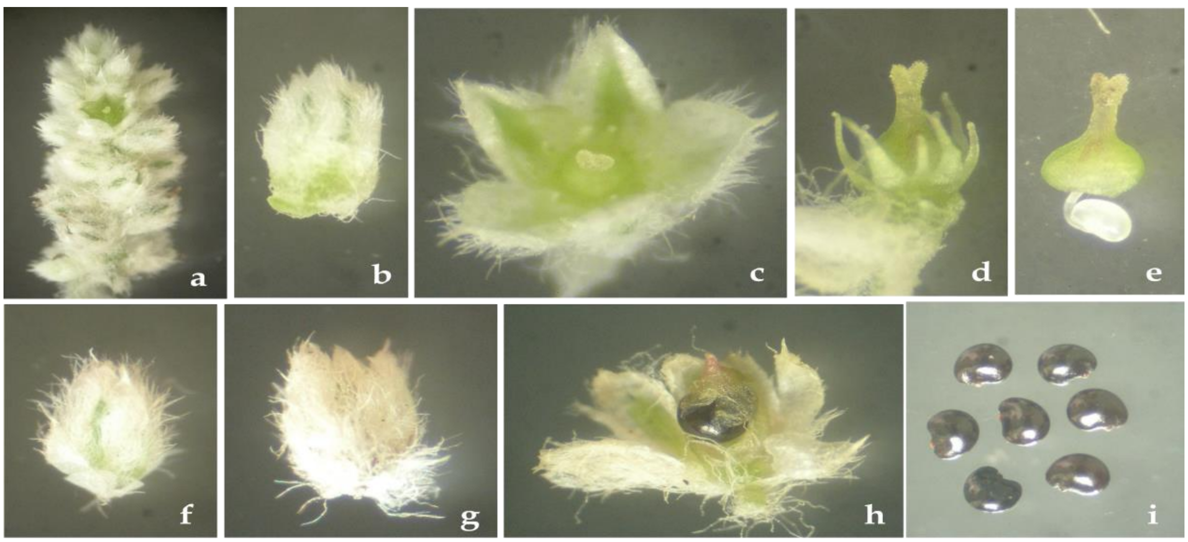

Figure 2. *Aerva lanata*: a. Inflorescence with female flowers, b. Female mature bud, c. Flower, d. Ovary with bifid stigma surrounded by staminodes, e. 1-ovuled ovary, f. & g. Fruits, h. 1-seeded fruit, i. Seeds.

Fruiting and seed dispersal: Fruit set rate in open pollinations was 98% in bisexual plants and 96% in female plants. In bisexual plants, spikes bagged prior to the production of first flowers set 35% fruit set while in female plants, spikes bagged prior to the production of first flowers set 57% fruit set. In both flower sexes, fruit and seeds are of same size and viable. Fruit is a minute circumscissile 1-seeded utricle, greenish-yellow, broadly ovoid, smooth, shining and enclosed by persistent perianth (Figure 2f-h). Seeds are black, kidney shaped, smooth and shining with coriaceous testa (Figure 2i). Seed dispersal occurs either by fruit dehiscence or by the fall of mature and dry fruited spikes rolling on the ground due to wind. Further, fruited spikes and dispersed seeds on the ground are dispersed by rain water during wet season. Seeds germinate as soon as they are dispersed if the soil is wet and germination rate is very high during wet season.

ALLMANIA NODIFLORA

Plant and flowering phenology: It is an annual herbaceous weed that grows in damp open sites and along roadsides (Figure 3a). At population level, it grows throughout the year in habitats with sufficient soil moisture. The stem is prostrate and covered with simple hairs. The leaves are glabrous, linear and narrowly elliptical. The flowering is profuse during wet season while it is sparse to sporadic in other seasons in areas where the soil is wet. Inflorescence is an axillary and terminal globose head consisting of several crowded flowers (Figure 3b-d).

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Figure 3. *Allmania nodiflora* – Yellow-flower form: a. Habit, b. & c. Inflorescences, d. Inflorescence with flowers.

Flower morphology: The flowers are short-stalked (Figure 4a), small (5.3 ± 0.5 mm long and 4.3 ± 0.4 mm wide), yellow with slight pink tinge, actinomorphic, odorless, bisexual and enclosed basally by 1 fleshy membranous bract and 2 papery bracteoles. The perianth is represented by five yellow tepals with pinkish tinge, free entirely and elliptic to lanceolate. The stamens are five, opposite to the tepals; their filaments are cream-colored, free but connate at the base enclosing the ovary (Figure 4g). The anthers are pink-colored, dithecous, introrse and glabrous. The ovary is monolocular with one erect ovule (Figure 4j,l). The style is filiform and glabrous with capitate shiny papillose wet stigma which is placed at the height of anthers (Figure 4i,j).

Floral biology: The flowers are open during 0600-1700 h with most opening during 0600-1100 h. In maturing bud, the anthers are placed well below the stigma and they reach to the height of the stigma by the time of anthesis (Figure 4b-f). Anthers dehisce during mature bud stage by longitudinal slits. The pollen grains are monads, creamy white, spheroidal, pantoporate and 22.14 ± 2.15 µm in diameter (Figure 4h). The stigma is receptive during anthesis and remains so until the noon of the next day. The nectar is secreted in traces around ovary inside the connate part of the stamens. The tepals close back on the evening of the next day. The bracts, bracteoles, tepals, style and stigma are persistent until seed dispersal while the stamens wither and perish inside the tepals during the growth and development of the fruit.

Spontaneous selfing: The flowers with the dehisced anthers and receptive placed at the same height resort to spontaneous selfing. The inflorescence heads bagged and followed for three weeks showed 25% fruit and seed set rate indicating that the plant is self-compatible and self-pollinating with vector-mediated pollination. During rainfall, the rain drops falling on the dehisced anthers knockout pollen grains resulting in the deposition of pollen on the stigma effecting self-pollination. As the plant forms a carpet of population especially in open areas, the anthesis of several flowers in each inflorescence head and the wind-driven light pantoporate pollen contribute to the occurrence of self- or cross-pollination.

Insect pollination: The floral buds were used by thrips for breeding and feeding. They moved out of the flowers during and after anthesis collecting nectar and pollen from the same or different inflorescence heads of the same and adjacent plants effecting self-pollination mostly and cross-pollination to limited extent. After flowers are open, they were visited by nectar and pollen collecting bees and nectar collecting wasps and butterflies day-long with more foraging activity during forenoon period. The butterflies included pierids, nymphalids and lycaenids. The foraging activity of all these insects effected self and/or cross-pollination.

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Fruiting ecology and seed dispersal: Fruits mature in three weeks (Figure 4a,b). The tepals bulge gradually covering the growing fruit while the tepals are enclosed by the bract and bracteoles. Natural fruit set is 80%. Fruit is a membranous and glabrous 1-seeded utricle (Figure 5c). The seeds are black, shiny and globose with a fleshy strophiole (Figure 5d). Fruits dehisce by circumscissile fashion exposing seeds; this dehiscence is characterized by the breaking of the papery fruit pericarp horizontally and causing the seed to slip and fall to the ground subsequently (Figure 5e). Seeds also disperse by wind on clear sunny days and by rain water on the days of heavy rainfall. During dry weather conditions, *Camponotus* and *Oecophylla* ants carried seeds to their nests where they consumed the fleshy strophiole and fed to their larvae without damaging the seeds (Figure 5f). Therefore, seed dispersal involves autochory, anemochory, ombrochory, hydrochory and myrmecochory.

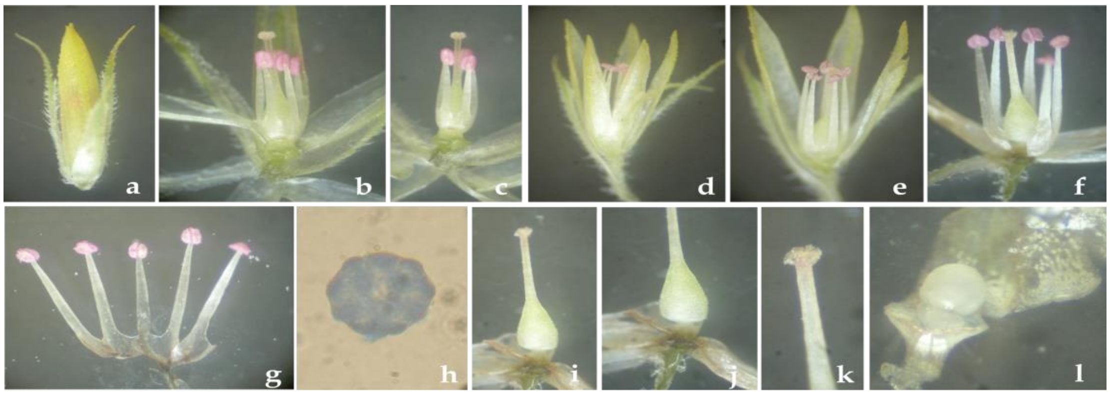

Figure 4. *Allmania nodiflora* – Yellow flower form: a. Mature bud, b. & c. Position of stigma in relation to anthers in mature bud stage, d-f. Equal position of stigma and stamens during anthesis, g. Stamens, h. Pollen grain, i. Pistil, j. 1-ovuled vary, k. Capitate stigma, l. Ovule.

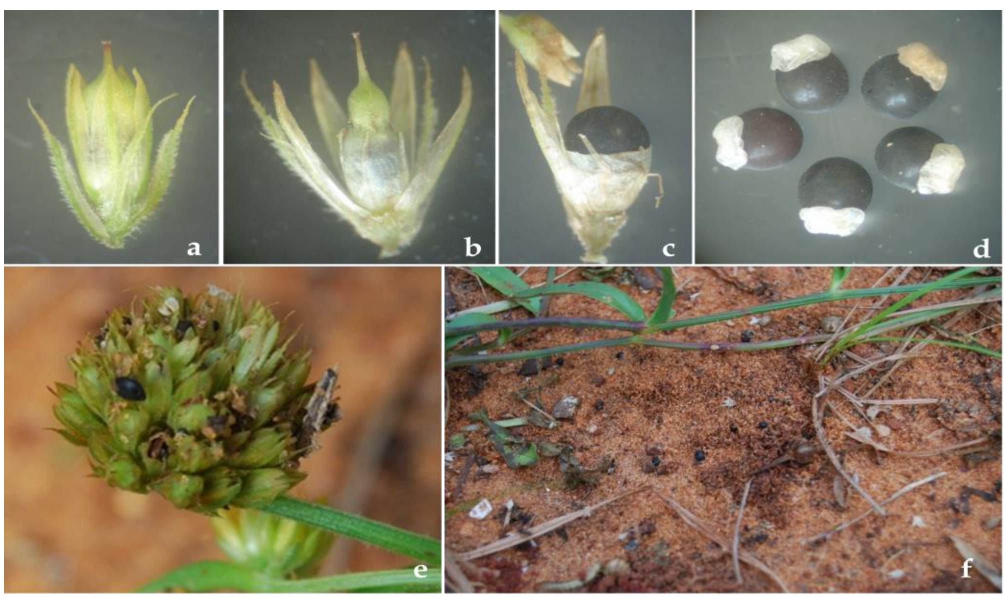

Figure 5. *Allmania nodiflora* – Yellow flower form: a. & b. Mature fruit, c. 1-seeded utricle, d. Seeds with strophiole e. Self seed dispersal, f. Seed dispersal by ants.

PUPALIA LAPPACEA

Phenology: It is a perennial erect to prostrate sprawling much-branched herb grows in the hedges of agricultural fields, fruit orchards, dry scrub forests, open dry sandy soils and waste lands. The stem is densely hispid and woody at the base. Leaves are petiolate, simple, vary in shape and size, ovate-elliptic, apiculate at the tip, opposite-decussate. The plant grows and reproduces through seed throughout the year in damp sites while it is seasonal in appearance in dry to semi-dry areas where it grows during

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rainy season (Figure 5a). The vegetative growth, flowering and fruiting is massive during wet season while it is moderate to sparse during winter and dry seasons in damp sites.

Flower morphology and biology: The inflorescence is terminal in position, 12-21 cm long, racemose forming alternate well-spaced triad woolly sessile flowers with 3 mm long lanceolate and acute bracts and 2 mm long villous, oblong bracteoles; both bracts and bracteoles are persistent and deflex after fruit fall. Each triad set consists of 1 hermaphrodite fertile flower (Figure 6b,c) escorted on each side by one modified sterile flower; both fertile and sterile flowers are nectarless. In both fertile and sterile flowers, the tepals are 5, woody, tri-nerved, 3-5.5 mm long, lanceolate to ovate, acute and villous. In fertile flowers, the stamens are 5, free but united into a fleshy, lobed cup at the extreme base; filaments are purple while anthers are white, dorsifixed, dithecous and introrse. Anthers dehisce during mature bud by longitudinal slits (Figure 6f). The pollen grains are light creamy white, spheroidal, peri-pantoporate with small pori covered star-shaped operculum and densely scabrate tectrum and 17.23 ± µm (Figure 6g,h). The pistil consists of 1-ovuled compressed ovary with simple style and capitate papillose stigma; the ovule is erect and pendulous (Figure 6i,j). The stigma is receptive during anthesis and remains so by the evening of the same day. The sterile flowers lacking staminodes are reduced to bunches of unequal stellately spreading hooked bristles.

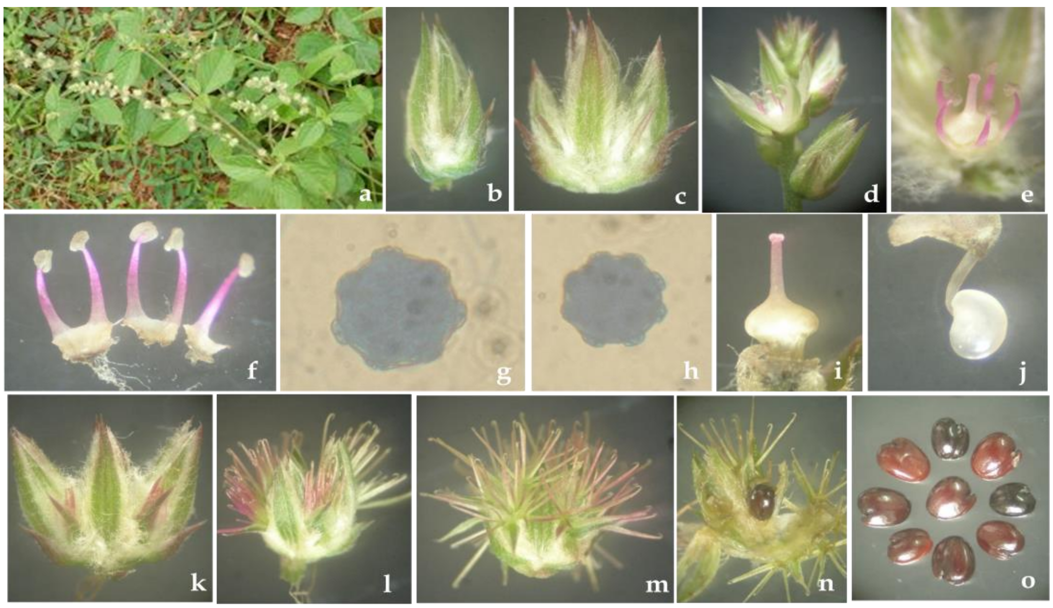

Figure 6. *Pupalia lappacea*: a. Flowering phase, b. & c. Mature bud, d. Flower, e. Position of stamens and stigma at the same height during flower phase, f. Dehisced stamens, g. & h. Pollen grains, i. Pistil, j. Ovule, k-m. Stages of fruit development, n. 1-seeded fruit, o. Seeds.

Pollination: Mature buds are open early in the morning indicated by the unfolding of tepals. The placement of introrse anthers and the stigma at the same height facilitates the occurrence of autonomous autogamy (Figure 6e) especially when the tepals close back by early evening and also anemophily as the stigma has the ability to capture the pollen with great ease by its papillae. Further, the flowers were visited sporadically by the stingless bee, *Trigona iridipennis* for pollen collection; its pollen collection activity ensures the occurrence of self or cross-pollination. The tepals close back enclosing the stamens, style and stigma inside and remain so persistently; the stamens gradually wither away inside the closed tepals while the style and stigma are persistent until fruit fall.

Fruiting and seed dispersal: Fruits from fertile flowers mature within two weeks following fertilization (Figure 6k-m). Fruit set rate is 98% in open-pollinations. Fruit is a depressed, globose 2-2.5 mm long 1-seeded indehiscent capsule tapering at the apex into the persistent style and stigma (Figure 6n), and covered with hooked bristles from sterile flowers. The seeds are dark brown to black, smooth, shining, ellipsoid and compressed (Figure 6o). Fruits of fertile flowers together with stellately hooked and spined sterile flowers fall as a "clustered burr" from the parent plant to the ground when mature and dry. The fallen fruits on the ground are dispersed by high winds during dry season and by rain water during wet season. The burred seed-heads with their reflexed hooks attach themselves to animals grazing in the area and are subsequently transported to new areas due to movement of animals. Further, the seed burrs with their sharp hooks stick to fur or clothing easily and are transported also by humans. After dispersal, the

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indehiscent fruit exposes the seed by decomposition of the fruit pericarp to enable its germination to produce new plant. During wet season, seeds germinate immediately and produce several batches of populations. In dry winter and dry season, seed germination is related to moisture status of the soil environment.

4. DISCUSSION

Aerva lanata

Gunatilake et al. (2012) reported that *Aerva lanata* is wide spread in the drier parts of the tropics and the sub-tropics of the world. Kirtikar and Basu (1996) mentioned that *A. lanata* is abundant on the plains in the warmer parts of India. In this study, it is found that *A. lanata* is distributed in damp open habitats, waste and disturbed areas and waysides which are characterized by semi-dry to dry areas. In these areas, it displays vegetative growth, flowering and fruiting depending on the soil moisture status but these phenological events occur consistently in habitats with enough soil moisture.

Khan et al. (1970) reported that *A. javanica* is dioecious with female plants as common and male plants as rare. It is primarily obligate apomictic producing seeds in the absence of pollen. This apomictic mode is important for its long range dispersal. *A. pseudotomentosa* is a hermaphroditic and its flowers display pollen and pollen germination on the pistil indicating that it is not an apomictic. Kapralov et al. (2012) reported that *A. lanata, A. leucura* and *A. sanguinolenta* are polygamous. Different authors documented that *A. lanata* is either bisexual or often bisexual (Warrier 1994; Athira and Nair 2017; Ranjan and Deokule 2013), dioecious (Nagaratna et al. 2014; Bitasta and Madan 2016), and is normally self-pollinated (Saxena and Brahmam 1994; Athira and Nair 2017). In the study area, *A. lanata* populations indicated that it is strictly dioecious with bisexual and female plants. High fruit set rate in open pollinations in bisexual plants indicate it is self-compatible and self- as well as cross-pollinating. Gravitational pollination, wind pollination and thrips and stingless bee pollination collectively contribute to the fruit set evidenced in this study in bisexual plants. Copious pollen production at flower level is advantageous for the plant to maximize pollination rate through self as well cross-pollination using abiotic and biotic pollinating agents. The highest fruit set in female plants is attributable to pollen flow from bisexual plants to female plants mediated by wind, thrips and stingless bees. Pantoporate spheroidal pollen grains appear to be an adaptation to cling to insect body and/or stigma surface (Livingstone et al. 1973). Since female flowers are devoid of pollen on their stigmas set fruit, it is indicative of the functionality of apomixis in female plants to maximize fruit set rate. Nectar production by both bisexual and female flowers is an indication that this plant is also adapted for pollination by thrips and insects, at the study sites only stingless bees. Gravitational pollination, anemophily, thripsophily and melittophily ensure *A. lanata* to maximize fruiting rate to facilitate long range dispersal. Further, apomixis in female flowers is a "fail-safe" strategy to produce fruits in the absence of wind and insects, especially during wet season in order to enhance fruit set rate and succeed as a prominent weed. This apomictic mode also facilitates the occurrence of genetic variation through mutation, auto-segregation and somatic crossover under varied environmental conditions (Khan et al. 1970). Further, the plant uses autochory, anemochory and hydrochory modes of seed dispersal which enable its widespread dispersal. Therefore, the functionality of sexual and asexual modes, and different seed dispersal modes ensure *A. lanata* to occupy different habitats and become a widespread weed.

Allmania nodiflora

A. nodiflora as an annual herbaceous weed reproduces exclusively by seed throughout the year if the soil is semi-wet or damp. The globose head inflorescence with several crowded yellow flowers with pinkish tinge on tepals and pink colored anthers are quite attractive and appear to have adaptation also to insect-pollination. Kajale (1940) and Costea et al. (2003) reported that self-pollination is not rare in Amaranthaceae family. Autogamy may occur if the anthers and stigma are in contact at a suitable time. The species displaying anthers at the height of style or slightly beyond the style are commonly pollinated by spontaneous autogamy than by wind. In this study, it is found that *A. nodiflora* flowers facilitate the occurrence of spontaneous autogamy due to the position of both stigma and dehisced anthers at the same height and nearly synchronous maturation of male and female sex organs.

Piotrowska (2008) stated that virtually all Amaranthaceae are wind-pollinated but the plants produce less pollen than other anemophilous species; this is compensated by the display of a longer flowering period. Muller and Borsch (2005) stated that although anemophily is common in Amaranthaceae, species of many genera are frequently visited by insects. Vividly coloured tepals with stellate pore ornamentation in certain taxa suggest insects as pollen vectors. In this study, *A. nodiflora* flowers exhibit a combination of anemophilous and entomophilous traits. The anemophilous characters are small flower size, absence of odor and short tepals (Niklas 1985) while the entomophilous characters are prominent tepals, production of nectar and well exposed colored anthers and stigma (Faegri and van der Pijl 1979). The stigma with capitate structure is capable of capturing pollen from the air

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prior to probing by foraging insects. The exposed state of stamens makes possible the pollen release from the anthers into the air which is then captured by the stigma. It is mostly likely that *A. nodiflora* produces less pollen than other anemophiles as it flowers and fruits yearlong if the soil is favourable. This moderate amount of pollen and minute volume of nectar indicate that the flowers are entomophilous also.

Borsch (1998) reported that *Allmania* exhibit *Deeringia*-type of pollen. Kajale (1940) reported that the pollen grains are multi-porate with 14-17 pores in *A. nodiflora*. In this study also, the pollen grains of *A. nodiflora* are multi-porate and these pores generate a high air turbulence to reduce the friction between the pollen grains and the air and maximize the distance to disperse them effectively (Franssen et al. 2001). The pollen grains contain starch which enables them to protect against desiccation (Roulston and Buchmann 2000) and this character is important to withstand dry spells and high winds during rainy season. The pollen grains have microspinules (Borsch 1998) which enable them to adhere to the stigma hairs (Costea et al. 2003). These pollen characters are important to achieve pollination by both wind as well as insects. Further, rain water/drops are also instrumental in effecting pollination by knocking out pollen from the anthers due to which pollen is most likely to reach the capitate stigma leading to the occurrence of pollination. Therefore, *A. nodiflora* flowers are structurally and functionally adapted for spontaneous autogamy, anemophily and ombrophily while keeping options open for entomophily.

In the present study, the minute volume of nectar produced in these flowers is mostly consumed by thrips which use the floral buds as breeding sites. The left-over nectar in the flowers is utilized by all nectar-feeding insects. bees, wasps and butterflies have been found to be effecting pollination in *A. nodiflora*. Bees use both pollen and nectar while other insects use only nectar as floral reward. Since this nectar is in traces during flower life, it drives these insects to pay multiple visits to flowering heads of the same or different individuals effecting self- and cross-pollination. Further, rain also causes selfing by the splashing rain drops into the flowers. Therefore, *A. nodiflora* is adapted for pollination by autonomous selfing, wind, insects and rain water.

Kapralov et al. (2012) reported that many genera in Amaranthaceae produce 1-seeded utricles with a firm apex bearing the style and very thin, membranous walls which is mostly likely an adaptation to the xerophytic conditions. In such conditions, during rainfall, the ripe seed in utricle swells, bursts the capsule and falls to the ground. In this study, *A. nodiflora* is 1-seeded utricle with a firm apex bearing the style and stigma and very thin, membranous pericarp. Borsch (1998) reported that a high proportion of Amaranthaceae produce dry capsular fruits which are open by irregular rupturing of thin walls. But, in species producing fruits with circumscissile mode of dehiscence produce black shining seeds with thin coat that shows an obscure reticulate pattern even when smooth. In this study, *A. nodiflora* dehisce by a circumscissile lid to disperse smooth, black shining seeds with thin coat that shows obscure reticulate pattern; only seeds fall to the ground while the tepals together with the bract and bracteoles remain attached to the parental plant. This finding is in disagreement with the report of Costea et al. (2003) that the species in which the fruit is a circumscissile capsule exhibits two layers in pericarp between which a large intercellular space exists and it is filled with air allowing the fruit to float. Since the seeds are exposed during the entire dry season in dry habitats, they should have insulation capability against desiccation. In this context, Costea et al. (2003) noted that such seeds are resistant to chemical and physical atmospheric agents until they show signs of germination in the wet season.

Costea et al. (2003) reported that seed dispersal in Amaranthaceae occurs by wind, water, animals and humans. In this study, it is found that *A. nodiflora* exhibits autochory, anemochory, ombrochory, hydrochory and myrmecochory. In this species, cushion-like strophiole developed underneath the seed is an elaisome which attracts *Camponotus* and *Oecophylla* ants. These ants transport seeds to the nest where they consume the elaisome or feed it to their baby ants after which they deposit the seeds in garbage piles of the nest or outside the nest. Edwards et al. (2006) stated that elaiosomes are rewards for ants like fruits or berries as rewards for vertebrate dispersers. Gorb and Gorb (2003) reported that myrmecochory provides the seed with protection from seed predators and a safe place for seed survival during unfavorable periods such as fires and/or a microsite rich in nutrients. Goldblatt (1997) stated that the physiological and energetic costs of producing elaiosomes are likely to be much smaller than producing fleshy fruits and hence elaiosomes are cheap to make. Milewski (1983) mentioned that ants need to be abundant at levels that guarantee that seeds will be picked up and the seed traits need to directly influence the subsequent fate of seeds. Under such conditions, a seed structure that has small physiological/energetic costs to produce but can manipulate ants into retrieving, dispersing and discarding the seed to a microsite suitable for germination and subsequent growth could increase plant fitness. This author also noted that myrmecochory may be favored by selection in more open, drier or less predictable habitats than in closed, wetter and more stable habitats due either to the higher availability of ants as opposed to vertebrates as dispersers or to the lower costs of developing a reward for dispersal. It is true in case of *A. nodiflora* which grows in open and less predictable habitats. Autochory, anemochory, ombrochory, hydrochory and myrmecochory enable *A. nodiflora* to colonize new habitats and become widespread as a successful weed.

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Pupalia lappacea

P. lappacea is a perennial sprawling herb and widespread in different habitats both in natural and cultivated lands. It has the ability to produce several generations in the same year in damp sites while a few generations in non-damp sites. The racemose inflorescence with triad flowers produced alternately on its axis is quite distinct from the foliage as it is produced in terminal position of the branch/stem. In this plant, only hermaphrodite flowers produce fruits/seeds while sterile flowers escort them and ensure their dispersal by different means. Such a placement of the inflorescence facilitates the occurrence of autonomous selfing either during anthesis or at the closing time of tepals because the anthers are freely exposed making the pollen dry and disperse easily between the stamens and stigma of the same flower. Further, wind also disperses the dry pollen across the flowers of the same or different racemes of the same or other individuals in the habitat effecting either self- and cross-pollination. The function of homogamy is also advantageous for the plant to resort to self or cross-pollination according to the pollen source. Livingstone et al. (1973) explained that the stellate pore ornamentation in pollen grains is an adaptation to cling to insect pollinators or to the stigmatic surface and the thickened structure over each pore is viewed as advantageous to taxa growing in xeric environments. Muller and Borsch (2005) noted that stellate pore ornamentation cannot be considered the only means to achieve pollination by insects but it is most likely a result of further specialization to particular pollen vectors and interaction with stigma. In this study, the stellate pore ornamentation in the pollen of *P. lappacea* could be advantageous to withstand adverse ambient environment in dry habitats and also to cling to insect pollinators for achieving vector-mediated pollination. But, only one stingless bee species, *Trigona iridipennis* is occasionally visiting the flowers of this species for pollen collection although there are several wild bee species in the habitat; this situation could be attributable to the production of pollen only from hermaphrodite flowers in each triad which requires skill by probing bees to search and recognize fertile flowers from sterile flowers to collect pollen and also it is not energetically profitable for the bees. *P. lappacea* despite having specialization in pollen grains is not able to attract insect pollinators due to production of a few fertile flowers per inflorescence and escorting of each fertile flower by a sterile flower on its both sides making it difficult for insect pollinators to probe fertile flowers for pollen collection. Therefore, *P. lappacea* is primarily anemophilous although self-pollinated autonomously and pollinated sporadically by the stingless bee.

In *P. lappacea*, the nearly cent percent fruit set recorded in open pollinations is relatable to the production of a single ovule by fertile flowers and the chances for the pollination of stigma and fertilization of ovule are very high through wind pollination and the fertile flowers are able to produce fruits with a single seed even with the receipt of a few pollen grains by the stigma. The indehiscent capsule-type fruit is 1-seeded and the seed coat is thick brown to black (Sukhorukov et al. 2015); its dispersal is associated with stellately hooked and spined sterile flowers because fruits disperse along with sterile flowers as a unit of "clustered burr". In this context, it is pertinent to mention the report by Di Vincenzo et al. (2018) that *Pupalia* genus is one of the youngest groups that have evolved modified sterile flowers with hooks forming adhesive diaspores. Ridley (1930) reported that *Pupalia* species have the diaspores as the most persistent adhesive burrs in order to be animal-dispersed by adhesion. Kapralov et al. (2012) reported that in *Pupalia*, the burr-like appendages of the fruits help to attach easily on the fur of animals for their dispersal. In this study, *P. lappacea* fruit disperse by wind (anemochory), rain water (hydrochory) and by adhesion to the fur of animals (epizoochory) and to the cloth of humans (anthropochory). Fruits decompose and expose seeds which germinate either immediately or later according to soil moisture status. The ability of the plant to produce several generations in the same year and the ability to grow in damp and dry habitats ensures its survival as a widespread weed and expand its distribution range in tropical latitudes.

5. CONCLUSION

Aerva lanata and Pupalia lappacea are perennial herbs while *Allmania nodiflora* is an annual herb. *A. lanata* is dioecious with bisexual and female plants while *P. lappacea* and *A. nodiflora* are hermaphroditic. In *A. lanata*, the bisexual flowers have five fertile stamens and five staminodes while female flowers have ten staminodes lacking anthers. In *P. lappacea*, the flowers are borne as triads with one hermaphroditic fertile flower and two sterile flowers alternately along the entire length of racemose inflorescence. *A. lanata* and *A. nodiflora* flowers are nectariferous while *P. lappacea* flowers are nectarless. In all three species, the pollen grains are spheroidal and pantoporate but *P. lappacea* pollen grains also have stellate pore ornamentation. In *A. lanata*, the stigma is papillose bifid stigma while in *A. nodiflora* and *P. lappacea*, the stigma is capitate papillose stigma enabling pollen capture from the anthers of the same flower by contact and the airborne pollen driven by wind. The hermaphroditic flowers of *A. lanata*, *A. nodiflora* and *P. lappacea* are homogamous and facilitate autonomous selfing as they are self-compatible and self-pollinating. In *A. lanata*, female flowers are apomictic which facilitates the occurrence of genetic variation through mutation, auto-segregation and somatic crossover under varied environmental conditions in female plants. Pollination also occurs by gravity within the flower, by wind and insects in *A. lanata,* by wind, insects and rain water in *A. nodiflora* and by wind and bees in *P. lappacea*. Fruit is a 1-seeded circumscissile dehiscent

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utricle in *A. lanata* and *A. nodiflora* while it is a 1-seeded indehiscent capsule which disperses along with sterile flowers modified into stellate hooks and spines in *P. lappacea*. In all the three species, autochory, anemochory and hydrochory are functional; additionally ombrochory and myrmecochory are functional in *A. nodiflora* and epizoochory and anthropochory in *P. lappacea*. Therefore, *A. lanata* with sexual and asexual modes, *A. nodiflora* and *P. lappacea* with only sexual mode, and all the three species with more than one pollination mode and seed dispersal mode are able to invade different habitats with varied environmental conditions and grow as widespread weeds in the tropics.

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Authors contributions
All three authors contributed equally.

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Ethical approval
The ethical guidelines for plants & plant materials are followed in the study for species collection & identification.

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