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Reproductive ecology of *Allmania nodiflora, Celosia argentea* var. *margaritacea*, and *Digera muricata* (Amaranthaceae)

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ABSTRACT: *Allmania nodiflora, Celosia argentea* var. *margaritacea*, and *Digera muricata* are annual herbaceous weeds which reproduce exclusively by seed. The plants appear in June, while flowering time is August-February in agricultural fields and August-October/November in other habitats. The synflorescence is an elongated erect spike in *A. nodiflora* and *C. argentea,* while it is a long pedunculate spicate raceme in *D. muricata*. The flowers anthese acropetally in *A. nodiflora* and *C. argentea* var. *margaritacea*, while there is no such clear-cut anthesis pattern in *D. muricata*. *Allmania nodiflora* is functionally hermaphroditic. *Digera muricata* is partially hermaphroditic because the central flower in three-flowered groups is fertile, while the lateral flowers are sterile. *Celosia argentea* var. *margaritacea* is functionally gynodioecious. In *A. nodiflora* and *D. muricata*, the flowers facilitate autonomous selfing due to synchrony in maturation of the male and female sex. In *C. argentea* var. *margaritacea* also, the flowers facilitate autonomous selfing, but it is precluded by strong protandry. All three species are anemophilous and entomophilous. *Allmania nodiflora* and *D. muricata* produce one-seeded fruits, while *C. argentea* var. *margaritacea* produces multi-seeded fruits. *Allmania nodiflora* and *C. argentea* var. *margaritacea* dehisce by means of a circumscissile lid and disperse seeds, while *D. muricata* produces indehiscent fruits. All three species are anemochorous, but *A. nodiflora* is also myrmecochorous.

Keywords: anemochory, anemophily, entomophily, gynodioecy, hermaphroditism, hydrochory, myrmecochory

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INTRODUCTION

Amaranthaceae Juss. (Caryophyllales Bercht. & J. Presl), in the traditional sense, includes about 70 genera and 800 species, which are mainly distributed in arid/semi-arid and saline habitats of tropical and subtropical regions of the world (Kadereit *et al.* 2003; Duretto & Morris 2011). Molecular investigations showed that this family forms a clade with Chenopodiaceae Vent. (about 110 genera and 1700 species) in the order Caryophyllales (Kadereit *et al.* 2003). Although further studies are necessary to resolve the taxonomic position of these two families, several authors followed the position taken by APG (1998), APG II (2003), APG III (2009), and APG IV (2016) in merging the two families (Uotila 2011; Sukhorukov 2013; Iamonico 2016).

Amaranthaceae s.str. includes species which have been of great interest to botanists, horticulturists, agriculturists, and laymen alike for a long time because of their importance as agricultural and food crops, vegetables, ornamentals, and medicine (Warrier *et al.* 1995; Salvador *et al.* 2004; Anilkumar 2006; Ravindra *et*

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al. 2008; Ogundipe & Chase 2009). Despite the multiple uses of Amaranthaceae species, studies about their reproductive biology are few. The importance of knowing the floral biology and pollination in Amaranthaceae members is related to their fast growth and invasive power. It is in this context that *Allmania nodiflora* (L.) R. Br., *Celosia argentea* L. var. *margaritacea* (L.) Iamonico (see Iamonico 2013), and *Digera muricata* (L.) Mart. were chosen for a study whose aims were to gain an understanding of: (1) how their floral morphology and biology, sexual systems, pollination syndromes, pollinators, and seed dispersal modes are functional in the habitats where they occur; and (2) how local insects use these plant species for food or breeding while reciprocating pollination services to them.

MATERIALS AND METHODS

Field surveys were carried out during the period 2013-2015 in Visakhapatnam and its surroundings, Andhra Pradesh, India (17°42′N and 82°18′E). Ten inflorescences were used to record the number of flowers per inflorescence; the flowers were counted manually. In the case of *C. argentea* var. *margaritacea,* length of the spike-like synflorescence together with the total number of flowers for each synflorescence was also recorded separately for bisexual and pistillate plants. Twenty-five fresh flowers were used to record the morphological characters. Ten premature inflorescences were tagged and followed daily to record the duration of flowering, the anthesis schedule, and the timing of anther dehiscence. Twenty-five fresh flowers were used to record the details of floral morphology. Nectar could not be measured and analysed due to its secretion in a minute quantity. Twenty mature, but un-dehisced anthers were collected from different plants and examined for pollen output as per the protocol described in Dafni *et al.* (2005). The pollen output and pollen-ovule ratio were determined according to Cruden (1977). Ten flowers per five individuals were used to test stigma receptivity following Dafni *et al.* (2005). Further, its receptivity was also judged visually by noting whether the stigma is shiny, wet, or withering. Insects foraging among the flowers were observed daily for a period of four days in order to establish their foraging behavior and role in pollination. Bees, wasps, flies, and bee-flies were identified by comparing with representative specimens available with the Department of Environmental Sciences, Andhra University, Visakhapatnam. Butterflies were identified by consulting the work by Kunte (2007). The foraging visits of insects were recorded on an area of 2 m^2 of a flowering patch for 10 min every hour throughout the entire day on four different days and the data were tabulated to record the foraging pattern and the percentage of visits made by them. Ten specimens of each insect species were captured during the peak foraging period, washed in ethyl alcohol, stained with aniline-blue on a glass slide, and observed under a microscope to count the number of pollen grains present and calculate the pollen carryover efficiency. Inflorescences that have not initiated flowering were tagged on the plants and followed to record the fruit and seed set rates in open pollinations. The fruit maturation period, morphological characteristics of the fruits, and those of the seeds were recorded to evaluate their adaptations for dispersal by different means. The role of wind and ants in fruit and seed dispersal was examined by visual means in the field. Aspects of seed germination and establishment were observed briefly in the field.

RESULTS

Allmania nodiflora

Plant habit, habitat, and phenology. This is a dichotomously branched annual herb that produces dense stands as an emergent weed in open wet soils, along road-sides, and in irrigated agricultural fields. Seeds germinate and produce new plants in the rainy season. The plants produce foliage by the end of July. Flowering time is in August-November, depending on the soil moisture status, with a peak during September. In irrigated agricultural fields, the flowering and fruiting extend until February. The plants disappear during March-May. The inflorescence is an axillary and terminal elongated head consisting of 74.8 ± 20.25 flowers which anthese acropetally for 8-10 days.

Flower. The flowers are short-stalked, small, greenish-white with a pink tinge at the anther sacs, actinomorphic, odorless, and bisexual. They are equipped with one fleshy membranous bract and two papery bracteoles. The tepals are five, narrowly elliptic-lanceolate, silvery membranous with a greenish white tinge, and entirely free. The stamens are five and opposite to the tepals; filaments are greenish-white, fused only at the base, and forming a cup-like structure enclosing the ovary. The anthers are dithecous, introrse, glabrous, and pink. The ovary is one-locular with an erect solitary ovule. The style is filiform, slender, glabrous, and extends into an obscurely two-lobed capitate shiny wet stigma; the stigma extends beyond the length of the tepals during flower life.

Floral biology. The flowers open from 7:00 to 17:00 h with a greater number between 7:00 and 10:00 h. The tepals unfold and expose the stamens and stigma following anthesis. Anther dehiscence occurs about half an hour prior to anthesis by longitudinal slits. The pollen output is 1423.4 ± 59.96 grains per anther and 7,117 per flower. The pollen: ovule ratio is 7117:1. The pollen grains are monads, white, spheroidal, 23.24 ± 3.32 μm in diameter, pantoporate and multiporate. The stigma is receptive from anthesis onwards to the next day. Nectar is produced in a minute volume around the base of the ovary, within the cup-like staminal tube. The tepals close back partially on the second day of anthesis. The bracts, bracteoles, tepals, style, and stigma are persistent and remain in their place until seed dispersal, while the stamens gradually wither inside as the fruit grows.

The flowers facilitate the occurrence of autonomous selfing during or for a few hours after anthesis due to the position of both the stigma and dehisced anthers almost at the same height. The simply bagged mature buds for three weeks showed 20% fruit and seed set, suggesting that the plant has autonomous autogamy. During rain, the rain drops falling on the flowers splash the dehisced anthers and the pollen flies off and is deposited on the stigmas, due to which self-pollination occurs. The style grows continually until it stretches out beyond the length of the tepals, which situation occurs by the morning of the second day. Such a distinct position of the receptive stigma enables the latter to capture pollen easily from the ambient environment and from foraging insects until the evening of this day.

Flower visitors and pollination. Thrips were found to be using the floral buds for breeding and flowers for feeding on nectar and pollen. The flowers were visited by bees, wasps, and butterflies from 8:00 to 17:00 h, with high activity during the forenoon. Bees collected both nectar and pollen in the same and/or different foraging visits, while wasps and butterflies collected only nectar. The bees were *Apis cerana* F., *A. florea* F., *Ceratina viridissima* Dalla Torre, *Ceratina* sp., and *Halictus* sp. The wasps were *Scolia quadripustulata* F., *Eumenes conica* F., *E. petiolatata* F., *Ropalidia* sp., *Rhynchium* sp., *Bembix* sp., and one unidentified wasp species. The butterflies were *Catopsilia pomona* F., *Eurema hecabe* L., *Phalanta phalantha* Drury., *Junonia lemonias* L., *Junonia hierta* F., *Tirumala limniace* Cr., *Danaus chrysippus* L., *Euploea core* Cr., *Castalius rosimon* F., *Leptotes plinius* F., *Zizula hylax* F., *Zizeeria karasandra* Moore, *Zizina otis* F., *Freyeria trochylus* Freyer, *Euchrysops cnejus* F., *Chilades pandava* Horsfield, *Prosotas dubiosa* Georg Semper, and *Spindasis vulcanus* F. (Table 1). Butterflies were more regular and consistent foragers compared to wasps and bees. Bees made 27%, wasps 23%, and butterflies 50% of total visits in a day (Fig. 1). Among butterflies, lycaenids were relatively more consistent foragers and made most of the foraging visits out of the total number visits by butterflies. All of these insect species landed on the elongated inflorescence head to probe flowers for the forage; while doing so, they invariably contacted the exposed stamens and stigma with their head and ventral side, thereby effecting self- and/or cross-pollination. In second-day flowers, the stigma's position beyond the length of the tepals enabled the foragers to contact it first and then the anthers to promote cross-pollination. Reduced levels of nectar in flowers due to foraging by thrips was found to be driving the insect foragers to increase their foraging activity, thereby raising the rate of cross-pollination. The body washings of all insect visitors revealed the presence of pollen to varying extents - from 35 to 325 grains on bees, from 19 to 103 grains on wasps, and from 16 to 113 grains on butterflies (Table 2). Thus, all insect foragers proved to be pollinators.

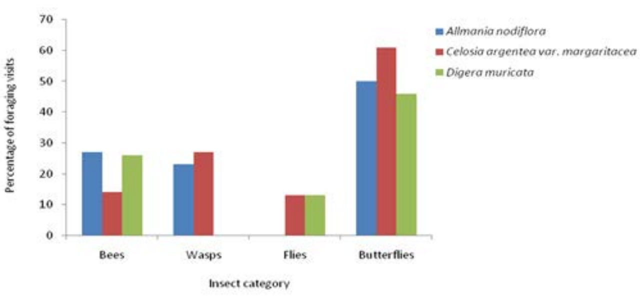

Fig. 1. Foraging visits by different categories of insects on the studied plant species, percentage of the total number of visits.

Fruiting ecology and seed dispersal. Fruits mature within 3 weeks. The tepals gradually bulge and cover the growing fertilised ovary; externally the tepals are surrounded by the bract and bracteoles. Natural fruit set is 76.35% and seed set is 61.35% (Table 3). Fruit is a membranous, glabrous utricle with a single, shiny, black, sub-globose, fleshy, strophioled seed. Seeds disperse easily due to their shiny and slippery nature. Fruits dehisce by means of a circumscissile lid which opens to disperse the seeds; in this dehiscence mode, the thin and papery fruit pericarp breaks horizontally and then the seed slips out and falls to the ground. Fruit dehiscence and seed dispersal occur acropetally in the elliptic heads from September to March. Seeds are dispersed by wind during dry spells during the rainy season. *Camponotus* ants were found to carry seeds to their nests, where they consume the fleshy strophiole or feed it to their larvae without damaging the seeds. Therefore, the plant is anemochorous and myrmecochorous. The plant reproduces exclusively by seed.

Celosia argentea var. *margaritacea*

Plant habit, habitat, and flowering phenology. This plant is an erect annual herb that forms many lateral roots to efficiently absorb nutrients from the soil. It forms dense stands as an emergent weed in open wet and dry soils, and in irrigated cultivated lands such as maize fields. The stem is branched, strongly ridged, and glabrous. Seeds germinate and produce new plants in June.

Table 1. List of insect foragers and the forage sought by them on the studied plant species.

Family	Insect name	*Allmania nodiflora*	*Celosia argentea* var. *margaritacea*	*Digera muricata*	Forage sought P: Pollen, N: Nectar
Hymenoptera					
Apidae	*Apis dorsata* F.	-	+	-	P + N
	Apis cerana F.	+	-	-	P + N
	Apis florea F.	+	-	+	P + N
	Ceratina viridissima Dalla Torre	+	-	-	P + N
Anthophoridae	*Xylocopa pubescens* L.	-	+	-	N
	Xylocopa latipes L..	-	+	-	N
	Ceratina sp.	+	-	-	P + N
Halictidae	*Halictus* sp.	+	-	-	P + N
Scoliidae	*Scolia quadripustulata* F	+	+	-	N
Chrysididae	*Stilbum superbum* Spinola	-	+	-	N
Eumenidae	*Eumenes conica* F	+	+	-	N
	Eumenes petiolata F	+	-	-	N
	Ropalidia sp.	+	-	-	N
Vespidae	*Rhynchium* sp.	+	+	-	N
	Wasp (Unidentified)	+	-	-	N
Crabronidae	*Bembix* sp.	+	-	-	N
	Stizus sp.	-	+	-	N
Diptera					
Syrphidae	*Helophilus* sp.	-	+	-	N
Calliphoridae	*Chrysomya megacephala* F.	-	+	+	N
	Fly (Unidentified)	-	+	-	N
Bombyliidae	Bee fly (Unidentified)	-	+	-	N
Lepidoptera					
Pieridae	*Catopsilia pomona* F.	+	-	-	N
	Eurema hecabe L.	+	-	-	N
Nymphalidae	*Acraea violae* F.	-	+	-	N
	Phalanta phalantha Drury	+	-	-	N
	Junonia lemonias L.	+	+	-	N
	Junonia hierta F.	+	-	-	N
	Junonia almana L.	+	+	-	N
	Hypolimnas misippus L.	-	+	-	N
	Tirumala limniace Cr.	+	+	-	N
	Danaus chrysippus L.	+	+	-	N
	Danaus genutia Cr.	-	+	-	N
	Euploea core Cr.	+	+	-	N
Lycaenidae	*Castalius rosimon* F.	+	-	-	N
	Leptotes plinius F.	+	-	-	N
	Zizula hylax F.	+	-	-	N

	Zizeeria karasandra Moore	+	-	+	N
	Zizina otis F.	+	-	+	N
	Freyeria trochylus Freyer	+	-	+	N
	Euchrysops cnejus F .	+	-	-	N
	Chilades pandava Horsfield	+	-	-	N
	Prosotas dubiosa George Semper	+	-	-	N
	Spindasis vulcanus F.	+	-	-	N
	Azanus jesous Guerin.	-	-	+	N
Hesperiidae	*Borbo cinnara* Wallace	-	+	-	N

Flowering time is August-February, with a peak during October. The plants disappear during March-May. The flowers are morphologically bisexual, but the floral details indicate that they are functionally gynodioecious. Individuals of both flower sexes occur in a ratio of about 1:1 in the same habitat. The inflorescence is a terminal solitary elongated erect spike with a conical apex. The length of spikes and number of flowers of those on the main stem and lateral branches varied in both bisexual and pistillate individuals. In bisexual plants, the spike of the main stem is 12.79 ± 4.84 cm long with 473.3 ± 97.56 flowers, while that of lateral branches is 5.44 ± 1.17 cm long with 172.3 ± 34.03 flowers. In pistillate plants, the spike of the main stem is 9.91 ± 1.81 cm long with 331.6 ± 57.94 flowers, while that of lateral branches is 4.85 ± 0.92 cm long with 168.66 ± 53.03 flowers. The flowering life of spikes of the main stem and lateral branches in bisexual plants is 20-25 days on the main stem and 10-12 days on the lateral branches. The flowers open acropetally in these spikes. The inflorescences are showy due to a mix of white and light pink colours displayed by the flowers.

The flower. The flowers of the inflorescences of both the main stem and lateral branches in both bisexual and pistillate plants are morphologically similar and uniform in size. The flowers are sessile, small, greenish-white with a pink tinge, actinomorphic, not smelling, and bisexual. They have one papery bract that is lanceolate, hyaline, and glabrous; and two papery bracteoles that are hyaline and glabrous. The tepals are five, free, elliptic-oblong, glabrous, and greenish-white with a pink tinge. The stamens are opposite to the tepals; the filaments are whitish-pink and fused at the base to form a cup-like structure enclosing the ovary. The anthers are dithecous, introrse, glabrous, and whitish-pink, but the anthers are empty in pistillate flowers. In both bisexual and pistillate flowers, the ovary is one-locular with the number of ovules ranging from 1 to 13, the mean number being 5.6 (most of the ovaries produced 4–8 ovules). The style is pink, glabrous, and extends into an obscurely two-lobed capitate shiny wet stigma, which stands almost at the height of the anthers during flower life.

Floral biology. In both bisexual and pistillate plants, the flowers open from 6:00 to 17:00 h, but most of them open between 7:00 and 10:00 h. The tepals unfold and expose the stamens and stigma following the anthesis. The anthers dehisce only in bisexual flowers and dehiscence occurs during anthesis through longitudinal slits. The pollen output is 1345.16 ± 79.14 grains per anther and 6,726 grains per flower. The pollen:ovule ratio is 706:1. The pollen grains in bisexual flowers are monads, white in colour, spheroidal, dry, powdery, psilate, 22.41 ± 2.31 μm in diameter, pantoporate, and multiporate. The stigma attains receptivity by diverging its lobes immediately after anthesis in pistillate flowers and after 8 hours of anthesis in bisexual flowers; in both flower sexes, the stigma ceases to be receptive by the evening of the second day. Nectar is produced in a small volume around the base of the ovary within the cup-like staminal tube in both bisexual and pistillate flowers. The tepals close back, completely covering the stamens and stigma by the evening of the day of anthesis, then slowly unfold again, exposing the stigma 1 mm beyond the length of the tepals in pollinated flowers; in this situation, the stamens gradually wither away and fall off after 3 days in both bisexual and pistillate flowers. The bract, bracteoles, tepals, style, and stigma are persistent.

In bisexual flowers, autonomous autogamy does not occur, even though the stigma and the dehisced anthers stand almost at the same height; this is owing to commencement of stigma receptivity late in the evening hours. The pollen deposited on an un-receptive stigma within the flower may effect pollination when it becomes receptive. During rain, the rain drops falling on flowers splash the dehisced anthers with the result that the pollen flies off and is deposited on the stigma, due to which self-pollination occurs if the stigma is receptive at that time. In pistillate flowers with empty anthers, there is no possibility of any mode of selfing, either autonomously or by rain. In bisexual flowers, the powdery and light pollen grains equipped with multiple pores fly off easily into the ambient environment. The distinctly hairy stigmatic lobes of both bisexual and pistillate flowers facilitate the capture of pollen easily from the ambient environment and from foraging insects.

Table 2. Pollen grains recorded in the body washings of insects on *Allmania nodiflora, Celosia argentea* var. *margaritacea*, and *Digera muricata*.

Insect species	***Allmania nodiflora***		***Celosia argentea* var. *margaritacea***		***Digera muricata***	
	Mean	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**
Apis dorsata			96.2	24.92		
Apis cerana	239.3	67.03				
Apis florea	218.8	57.84			61.3	24.63
Ceratina viridissima	83.8	13.01				
Ceratina sp.	71.2	20.76				
Xylocopa latipes			56.55	17.78		
Xylocopa pubescens			64.5	26.99		
Halictus sp.	59.5	17.09				
Scolia quadripustulata	62.8	19.67				
Scolia sp.			61.8	26.41		
Scolia sp.			42.5	18.93		
Stilbum superbum			43.9	16.51		
Eumenes conica	56.9	18.45	38.6	12.06		
Eumenes petiolata	54.8	14.64				
Ropalidia sp.	46.3	12.12				
Rhynchium sp.	59.5	15.62				
Bembix sp.	46.9	12.48				
Stizus sp.			39.5	14.32		
Wasp (unidentified)	57.8	13.20				
Chrysomya megacephala			34.1	14.12	41.2	9.21
Helophilus sp.			33.8	15.21		
Fly (unidentified)			39.2	15.41		
Bee-fly (unidentified)			27.8	11.22		
Acrae violae			36.9	19.21		
Catopsilia pomona	63.2	14.48				
Eurema hecabe	59.2	16.37				
Phalanta phalantha	71.5	19.33				
Junonia lemonias	76.4	22.33	47.6	17.16		
Junonia alamana			36.1	16.33		
Junonia hierta	49.5	16.80				
Hypolimnas misippus			52.6	22.25		
Tirumala limniace	75.3	17.14	44.0	18.76		
Danaus chrysippus	86.5	18.96	61.3	19.78		
Danaus genutia			41.6	14.16		
Euploea core			45.6	18.66		
Castalius rosimon	62.3	17.42				
Leptotis plinius	59.4	16.95				
Zizula hylax	42.2	12.35				

Zizeeria karasandra	71.7	20.84			52.8	19.33
Zizina otis	56.9	14.71			47.9	17.70
Freyeria trochylus	52.3	13.61			61.9	21.56
Euchrysops cnejus	43.2	13.27				
Chilades pandava	63.5	17.26				
Prosotas dubiosa	46.4	11.52				
Spindasis vulcanus	59.8	16.10				
Azanus jesous					68.1	21.85
Borbo cinnara			32.8	12.92		

Flower visitors and pollination. The floral buds of both bisexual and pistillate plants were found to be breeding sites for thrips. Thrips were nectar and pollen foragers. The bisexual and pistillate flowers occurring on different plants were visited by the same species of bees, wasps, flies, bee-flies, and butterflies from 8:00 to 17:00 h, with concentrated activity during the forenoon period. The bees were *Apis dorsata* F., *Xylocopa latipes* L., and *X. pubescens* L. The wasps were *Stilbum superbum* L., *Rhynchium* sp., *Scolia* sp., *Eumenes conica*, and *Stizus* sp. The flies were *Chrysomya megacephala* F., *Helophilus* sp., and two unidentified fly species. The butterflies were *Acraea violae* F., *Junonia lemonias* L., *J. almana* L., *Hypolimnas misippus* L., *Tirumala limniace* Cr., *Danaus chrysippus* L., *D. genutia* Cr., *Euploea core* Cr., and *Borbo cinnara* Wallace (Table 1). Among bees, *A. dorsata* gathered both pollen and nectar, while *Xylocopa* species collected only nectar. All other insect species foraged for nectar only. All these insect species visited the flowers of both bisexual and pistillate plants alternately. However, wasps and nymphalid butterflies were more regular and consistent foragers when compared to other insects. Bees made 14%, wasps 27%, flies 13%, and butterflies 46% of the total number of visits in a day (Fig. 1). All of these insect species landed on the spike inflorescence of bisexual and pistillate plants to probe the individual flowers for forage; while doing so, they invariably contacted the exposed stamens and stigma with their head/ventral side/proboscis and thereby effected pollination. Reduced levels of nectar in the flowers due to nectar feeding by thrips was found to drive all insect foragers to increase their foraging visits and escalate the rate of pollination across pistillate and bisexual plants. The body washings of all insect visitors revealed the presence of pollen to varying extents - from 23 to 127 grains were obtained from bees, from 11 to 102 grains from wasps, from 10 to 61 grains from flies, 27.8 grains from bee-flies, and from 32.8 to 61.3 grains from butterflies (Table 2). Thus, all insect foragers were carriers of pollen to different extents and contributed to both self- and cross-pollination.

Fruiting ecology and seed dispersal. Fruits mature within 3 weeks in both bisexual and pistillate plants. The tepals gradually bulge and cover the growing fertilised ovary; externally the tepals are surrounded by the bract and bracteoles. In bisexual plants, the natural fruit set is 77.10% and seed set is 55.39%. In pistillate plants, the natural fruit set is 82.72% and seed set is 57.09% (Table 3). The fruit is a membranous, glabrous utricle with shiny, black, globose, compressed seeds. Each fruit produces 1–9 seeds. Seeds disperse easily due to their shiny and slippery nature. Fruits dehisce by means of a circumscissile lid to disperse the seeds; in this dehiscence mode, the membranous fruit pericarp breaks horizontally, after which the seed slips out and falls to the ground. Fruit dehiscence and seed dispersal occur acropetally in the spikes from September to March. Seeds are dispersed by wind during dry spells in the rainy season. Therefore, seed dispersal is anemochorous. The plant reproduces exclusively by seed.

Digera muricata

Plant habit, habitat, and flowering phenology. *Digera muricata* is an erect annual herbaceous weed that produces dense stands in open wet soils, along roadsides, and in irrigated agricultural fields. Seeds germinate and produce new plants during the rainy season. The flowering season varies with the habitat type: it is from August to November for plants occurring in open areas and along roadsides, but from August to February for plants growing on agricultural lands and in areas where the soil is sufficiently wet. The plants disappear in March. The inflorescence is a long, pedunculate, axillary, and spicate raceme-like structure, 10-15 cm long with numerous flowers; three flowers are produced at each point, of which the central one is fertile, while the other two are infertile with a single bracteole. Bracteoles are two and modified into accrescent antler-shaped scales during the fruiting phase.

The flower. The central fertile flowers are sessile, glabrous, small, tri-coloured (green, white, and pink), ac-

Table 3. Natural fruit and seed set rates in the studied plant species.

Plant species	No. of flowers sampled	No. of flowers that set fruit	Fruit set (%)	Seed set (%)
Allmania nodiflora	1666	1272	76.35	61.35
Celosia argentea var. *margaritacea*				
Bisexual flowers	166	128	77.10	55.39
Pistillate flowers	110	91	82.72	57.09
Digera muricata	741	698	94.19	94.19

tinomorphic, not smelling, and bisexual. The tepals are five, free, elliptic-lanceolate, greenish-pink, unequal, the outer two larger than the inner ones, oblong-lanceolate with an acute apex. The stamens are five, opposite to the tepals, whitish-pink, fused only at the base to form a cup-like structure enclosing the ovary. The anthers are dithecous, introrse, glabrous, and pink. The ovary is glabrous, uni-locular with a single ovule lateral on a curved funicle. The style is slender, glabrous, pink, and extends into a shiny wet two-lobed hairy divergent stigma.

Floral biology. The flowers open between 7:00 and 10:00 h, with most opening at 8:00 h. The stamens are located well below the height of the stigma during the bud stage, but stand almost at the height of the stigma at anthesis. The tepals unfold to expose the sex organs following anthesis. During anthesis, anthers dehisce through longitudinal slits and the stigma becomes receptive; the stigma ceases to be receptive on the evening of the same day, by which time the tepals close back. The pollen output is 274.6 ± 32.62 grains per anther and 1,373 grains per flower. The pollen:ovule ratio is 1,373:1. The pollen grains are monads, white, spheroidal, 32.47 ± 6.89 µm in diameter, pantoporate, multiporate, dry, and fall as single grains. Nectar is produced in a small volume around the base of the ovary inside the cup-like staminal tube. The sterile flowers, bracteoles, tepals, style, and stigma are persistent and remain so until seed dispersal, while the stamens gradually wither inside as the fruit grows.

The flowers are such that they facilitate the occurrence of autonomous selfing and produce 70% fruit and seed set in simply bagged mature buds. During rain, rain drops falling on the flowers splash the dehisced anthers causing pollen to adhere to the stigmatic lobes, due to which self-pollination occurs. Being light in weight and dry, the pollen disseminates into the ambient air, and circulating wind effects both self- and cross-pollination.

Flower visitors and pollination. The floral buds were found to be breeding sites for thrips. The thrips were nectar and pollen foragers. The flowers were visited by the bee *Apis florea* for pollen and nectar, and by the fly *Chrysomya megacephala* and the lycaenid butterflies *Zizeeria karasandra, Zizina otis, Freyeria trochylus*, and *Azanus jesous* Guerin for nectar from 8:00 to 14:00 h, with more foraging activity during forenoon period. The bee and the fly were not constant and regular foragers, but all butterflies were regular and constant foragers. The soft and delicate inflorescence with minute flowers appeared to be appropriate for collection of nectar by the small lycaenid butterflies. The overall foraging activity of insects was considered to result in both self- and cross-pollination. Bees made 26%, flies 13%, and butterflies 61% of the total visits made in a day (Fig. 1). All these insect species landed on the inflorescence to probe the individual flowers for the forage; while doing so, they invariably contacted the exposed stamens and stigma with their head/ventral side/proboscis. The body washings of all insect visitors revealed that *A. florea* carried a mean number of 61.3, *C. megacephala* 41.2, and butterflies from 47.9 to 68.1 pollen grains (Table 2). It follows that all insect foragers were pollinators.

Fruiting ecology and seed dispersal. Fruits mature within 3 weeks. The tepals gradually bulge, exposing the persistent wilted bifid stigma, and cover the growing fertilised ovary; externally the tepals are surrounded by two sterile unibracteolate lateral flowers and bracteoles. The sterile flowers and bracteoles modify into an antler or a wing-like structure by the time the fruits mature. Natural fruit set and seed set are the same due to the production of a single ovule per flower and comprised 94.19% (Table 3). The fruit is a thick utricle that is membranous andglabrous and has a single sub-globose, ridged, green- to brown-coloured seed with a thick coat. The fruits mature acropetally and fall off in the same way; to be specific, they fall off together with modified sterile flowers and bracteoles. The fallen fruits decompose and expose the seeds during the rainy season. Due to their light weight, the fruits are dispersed by wind during dry spells within the rainy season. Seed dispersal is therefore anemochorous. The plant propagates exclusively by seed.

DISCUSSION

Allmania nodiflora, Celosia argentea var. *margaritacea*, and *Digera muricata* are annual herbaceous weeds which reproduce exclusively by seed. They form pure stands or mixed populations. The seeds respond to the first rains by germination and production of new plants. In all, their flowering takes place continually from August to February in agricultural fields and is terminated by October/November in other areas where the plants occur. On the basis of the obtained results, it can be asserted that length of the flowering season is habitat-specific and appears to be related to the moisture and nutritional status of the soils. Plants growing in agricultural areas exhibit robust growth, whereas those growing in other areas exhibit thin growth. The ability to grow in different habitats with varying levels of soil moisture and nutrients characterises them as successful major weeds.

Kapralov *et al.* (2012) stated that in Amaranthaceae the basic unit of the synflorescence is the cyme, and that simple or compound cymes are normally arranged along a central axis to form a characteristic spiciform or capitate structure (see also Acosta *et al.* 2009; Iamonico 2015). The synflorescences are either axillary or terminal in position in *A. nodiflora,* only terminal in *C. argentea* var. *margaritacea*, and only axillary in *D. muricata*. The flowers anthese acropetally in the first two species, while there is no such clear-cut anthesis pattern in *A. nodiflora*. *Celosia argentea* var. *margaritacea* displays several branches per individual, each branch having a terminal synflorescence. In *A. nodiflora* and *C. argentea* var. *margaritacea*, the synflorescences have an elongated erect or spike-like head, while in *D. muricata* they are long, pedunculate, and arranged in spicate raceme-like structures. Individual plants of *C. argentea* var. *margaritacea* possess either bisexual or pistillate flowers, and on this basis the plants are classified as bisexual plants and pistillate plants. In these plants, there is variation in length of the spike, which is longest in bisexual plants and shortest in pistillate plants. Moreover, the spike of the main stem (called the "main florescence" by Acosta *et al.* 2009) is the longest. In bisexual and pistillate plants, the main florescence produces more flowers than lateral spikes. In *A. nodiflora*, a synflorescence produces 75 flowers only, whereas in *D. muricata* the spicate raceme at each point produces three flowers, of which only one is prominent and functional.

Anilkumar (2006) stated that the synflorescences of *Amaranthus* and *Celosia* produce sterile flowers together with fertile flowers. Further, strongly modified sterile flowers occur in *Digera*. In the present study, the synflorescences of *A. nodiflora* are very compact and have flowers as clusters, all being fertile. In *C. argentea* var. *margaritacea*, the flowers are visually bisexual, but there is suppression of the male sex by the production of blank anthers without any pollen during subsequent development in half of the individuals of a population. In fact, this species maintains an almost one to one ratio of bisexual to pistillate plants at the population level. In *D. muricata*, the synflorescence presents flowers as three-flowered groups in which the central flower is prominent and fertile, while the lateral flowers are inconspicuous and sterile. Therefore, each synflorescence displays one third fertile flowers and two thirds sterile flowers, both of which have a role at the time of seed dispersal.

Kajale (1940) and Anilkumar (2006) stated that the flowers of Amaranthaceae are unisexual or bisexual, and that the plants display monoecious, dioecious, or polygamous sexual systems. Allogamy by dichogamy is said to be the norm in this family. Further, protogyny is functional as a way to achieve cross-pollination in species with hermaphroditic flowers and in those demonstrating monoecism. In the present study, *A. nodiflora* and *D. muricata* produced all functionally bisexual flowers typical of hermaphroditism, while *C. argentea* var. *margaritacea* dispslayed gynodioecy.

Kajale (1940) and Costea *et al.* (2003) asserted that self-pollination is not a rare occurrence in Amaranthaceae members. Autogamy may occur if the anthers and stigma are in contact at a suitable time. In those species where the anthers stand at the height of the style or slightly beyond the style, self-pollination is more common than anemophily. The touching of the stigma itself by stamens further promotes the occurrence of autonomous autogamy. In the present study, it was found that the flowers facilitate the occurrence of autonomous selfing during or for a few hours after anthesis due to the position of both stigma and dehisced anthers at almost the same height and virtual synchrony in the maturation of male and female parts in *A. nodiflora* and *D. muricata.* In *C. argentea* var. *margaritacea* also, such a situation exists to facilitate autogamy in bisexual plants, but it does not occur since the stigma commences its receptivity in the evening of the day of anthesis; however, it may occur if the pollen deposited on an un-receptive stigma is viable, allowing pollination during the receptive phase of the stigma. There is no possibility for autogamy or any form of selfing in pistillate plants due to non-production of pollen in their anthers.

Kajale (1940) considered that most species of Amaranthaceae are anemophilous. Piotrowska (2008) stated that virtually all Amaranthaceae are wind-pollinated, but the plants produce less pollen than other anemophilous species; this is compensated by their having a longer flowering period. Carinanos *et al.* (2014) noted that pollen production and release in Amaranthaceae tend to be very low, reflecting the pollen economy characteristic of xerophytic species, which minimise energy output to match resource availability. Pollen production is regulated not only by plant-intrinsic factors, but also by the environmental conditions in which the plants grow. Ia-

MONICO (2010) asserted that *Amaranthus retroflexus* L. is mainly pollinated by wind. COSTEA *et al.* (2003) noted that pollination in this species can be indirectly accomplished by insects because certain predators sometimes pick up insects carrying pollen grains, thereby effecting their dispersal. MULLER & BORSCH (2005) stated that although anemophily is considered to be the norm in Amaranthaceae, the vividly coloured tepals in taxa such as *Mechowia* Schinz with stellate pore ornamentation also suggest that insects can serve as pollen vectors. BORSCH (1998) noted that flowers which possess pollen of the *Ptilotus*-type are always showy, and in this connection he concluded that the pollenkitt may serve in insect pollination. The species concerned possess bright red or violet flowers. Consequently, they must possess a pollination syndrome that is composed of showy, betalain-coloured flowers attracting insects capable of discriminating red-violet colours, and of pollen grains that provide mechanisms for becoming easily transported. There are indications that white or cream-coloured flowers of many genera are insect-pollinated. KUBITZKI *et al.* (1994) mentioned that entomophily, particularly by bees, appears to play an undoubted part. These authors noted that *Perdita cladothricis* Cockerelle visits the flowers of *Cladothrix cryptantha* S. Wats., while *Melipona* bees visit the flowers of *Amaranthus spinosus* L.

In the present study, the flowers of all the three species display a mix of anemophilous and entomophilous morphological traits. In *A. nodiflora*, the anemophilous characters are small flower size, absence of smell, and short tepals (see NIKLAS 1985), while the entomophilous characters are prominent tepals, production of nectar, well exposed coloured anthers and stigma, projection of the stigma away from the tepals on the second day of anthesis, and economic production of pollen (FAEGRI & VAN DER PIJL 1979). The flowers display weak protandry and facilitate self- and cross-pollination on the day of anthesis, but stigma receptivity on the second day largely facilitates out-crossing. The capitate stigma is capable of capturing pollen from the ambient environment and from foraging insects prior to probing by the latter. The exposed stamens facilitate release of pollen from the dehisced anthers into the air, and the pollen thus released may be captured by the stigma. The moderate amount of pollen and minute volume of nectar indicate that the flowers are also adapted for pollination by insects. In *C. argentea* var. *margaritacea*, the anemophilous characters are small flower size, absence of odour, and short tepals, while the entomophilous characters are production of nectar, possession of a well exposed coloured style and stigma, projection of the stigma away from the tepals on the second day of anthesis, and economic production of pollen. In this species, the bisexual plants display strong protandry, while the pistillate plants display stigma receptivity immediately after anthesis; however, both plant sexes terminate stigma receptivity by the evening of the second day. The bisexual flowers are functionally staminate on the day of anthesis, the pistillate plants on the second day. Further, fruit and seed set rates show that a significant percentage of seeds are inviable due to non-filling, which is the highest in bisexual plants, indicating that the plant is primarily out-crossing (as is substantiated by inviable seed production through geitonogamy in bisexual plants) and that pollination is performed by both wind and insects. The two-lobed stigma with dense hairy growth is capable of capturing pollen from the ambient environment and from foraging insects prior to probing by the latter. In *D. muricata,* the small size of flowers, shortness of tepals, and absence of smell are anemophilous characters, while the production of nectar, colouration of all floral parts, and possession of a well exposed stigma are entomophilous characters. The termination of stigma receptivity and closure of the flower by the end of the day suggest that the plant is primarily self-pollinating, while keeping the options open for cross-pollination, which is achieved by both wind and insects. The flowers with a hairy stigma standing at or above the tepals capture pollen from the air and from foraging insects prior to probing by the latter. The pollen is dry and disseminates into the air easily due to the well exposed dehisced anthers. BORSCH (1998) reported that *Allmania, Celosia*, and *Digera* exhibit *Deeringia*-type pollen. KAJALE (1940) noted that the pollen grains have 14-17 pores in *A. nodiflora* and 15-20 pores in *C. argentea*. The present study indicates that the pollen grains of all the three plant species are multi-porate. The distribution of these pores on the pollen grains generates high air turbulence, which reduces friction between the pollen grains and the air, maximising the distance over which the pollen grains can be dispersed (FRANSSEN *et al.* 2001). The pollen grains contain starch, which protects them against desiccation (ROULSTON & BUCHMANN 2000), and this character is important because it enables them to withstand dry spells and high winds during the rainy season. BORSCH (1998) noted that the pollen grains of these species have microspinules, while COSTEA *et al.* (2003) stated that these structures enable pollen grains to adhere to stigma hairs. These characters are important since they allow the plant to achieve pollination both by wind and by insects. Thus, it appears that the three studied species possess flowers that are structurally and functionally adapted to anemophily, while keeping options open for entomophily.

We found pollination to be effected by bees, wasps, and butterflies in *A. nodiflora*; by bees, wasps, flies, bee-flies, and butterflies in *C. argentea* var. *margaritacea*; and by bees, flies, and butterflies in *D. muricata*. With the exception of *Xylocopa*, bees use both pollen and nectar, while *Xylocopa* and all other insect categories use only nectar as floral reward(s). In *Xylocopa,* male bees collect only nectar, while female bees collect both pollen and nectar for brood provisioning. *Xylocopa* bees collect pollen only from certain plant species such as *Cassia* spp., whereas they collect nectar from a number of plant species (Solomon Raju & Rao 2006). In the present study, *Xylocopa* bees used *C. argentea* var. *margaritacea* as a nectar source only. Among nectar foragers, wasps and butterflies are important pollinators for *A. nodiflora* and *C. argentea* var. *margaritacea*. Among butterflies, nymphalids and lycaenids are important pollinators for *A. nodiflora*, nymphalids for *C. argentea* var. *margaritacea*, and lycaenids for *D. muricata*. The flowers are important as a major pollen source for bees, but as a source of nectar for all other insects. 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 used by all nectar-feeding insects. Since this nectar is present only in traces during the flower's life, these insects are driven to pay multiple visits to flowering inflorescences of the same or different individuals of each plant species, due to which both self- and cross-pollination occur. Their role in pollination is highlighted by the body washings of all these insects. Further, rain also causes self-pollination by the splashing of rain drops into the flowers of these species. Thus, the sexual systems functional in *A. nodiflora* and *D. muricata* are adapted for pollination by autonomous selfing, wind, insects, and rain water, while those functional in *C. argentea* var. *margaritacea* are adapted for pollination by wind, insects, and rain water.

Kapralov *et al.* (2012) stated that many Amaranthaceae genera produce one seed per fruit with a firm apex bearing the style and very thin membranous walls, which appear to be an adaptation to the xerophytic conditions in which most species with fruits of this nature grow: when rains come, the ripe seed swells, bursts the capsule, and falls to the ground. In the present study, *A. nodiflora* and *D. muricata* were found to produce one-seeded fruits due to production of a single ovule per flower, while *C. argentea* var. *margaritacea* produced one to nine seeds against the production of 1-13 ovules per flower in both bisexual and pistillate plants. In *A. nodiflora* and *C. argentea* var. *margaritacea*, the fruits have a firm apex bearing the style and stigma and a very thin membranous pericarp. In *D. muricata*, the fruit and seed are inseparable, indehiscent, and have a firm apex bearing the style and stigma. Borsch (1998) wrote that several Amaranthaceae have dry capsular fruits which open by irregular rupturing of their thin walls. The species with circumscissile dehiscent fruit lids produce black shining seeds with a thin coat that shows an obscure reticulate pattern even when smooth. In the present study, fruits of *A. nodiflora* and *C. argentea* var. *margaritacea* were found to dehisce by means of a circumscissile lid to disperse shining smooth black seeds with a thin coat that displays an obscure reticulate pattern; only the seeds fall to the ground, while the tepals together with the bract and bracteoles remain intact on the parental plants. This finding is in disagreement with statements made by Costea *et al.* (2003) to the effect that species in which the fruit is a circumscissile capsule display two layers in the pericarp, between which a large intercellular space exists and is filled with air, allowing the fruit to float. Since the seeds are exposed during the entire dry season, they must have some kind of insulation against desiccation. 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. In the case of *D. muricata*, the indehiscent fruit with seed inside falls off from the parental plants, together with the tepals, antler-like bracteoles, and sterile flowers. The structures accompanying the indehiscent fruit appear to play a role in its dispersal on the ground (Anilkumar 2006). The hard fruit wall appears to be an adaptation to inhibit the loss of moisture during the dry season (Kapralov *et al.* 2012).

Costea *et al.* (2003) asserted that seed dispersal in Amaranthaceae is performed by four main factors: wind, water (river, water courses, and irrigation channels), animals, and humans. In the present study, it was found that *A. nodiflora* exhibits anemochory and myrmecochory. In this species, a cushion-like strophiole developed underneath the seed represents an elaiosome that attracts *Camponotus* ants, who transport the seeds to their nest. These ants consume the elaiosome or feed it to their young, after which they deposit it in garbage piles either in or outside the nest. Edwards *et al.* (2006) stated that elaiosomes function as rewards for ants in much the same way as fruits or berries serve as rewards for vertebrate dispersers. Gorb & Gorb (2003) wrote that myrmecochory protects the seed from seed predators, providing a safe place for survival of seeds under unfavourable conditions such as those created by fires and/or ensuring a microsite rich in nutrients. Goldblatt (1997) stated that the physiological and energy costs of developing elaiosomes are likely to be much lower than the costs of developing fleshy fruits, making their development cheaper. Milewski (1983) noted that ants need to be abundant at levels which guarantee that seeds will be picked up and that their traits need to directly influence the subsequent fate of seeds. Under such conditions, a seed structure that requires low physiological/energy costs to produce but can manipulate ants into retrieving, dispersing, and discarding the seed to a microsite suitable for germination and growth could increase plant fitness. That author also stated that myrmecochory may be favoured by selection in more open, drier, or less predictable habitats rather 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. This is true in the case of *A. nodiflora*, which grows in open and less predictable habitats. The anemochory and myrmecochory functional in this species enable it to colonise new environments or habitats. In *C. argentea* var. *margaritacea* and *D. muricata*, the seeds do not have elaiosomes and hence myrmecochory is ruled out. These plant species are exclusively anemochorous and functional during dry soil conditions. All three plant species propagate seasonally during the rainy season.

Takuya *et al.* (2008) stated that weeds have several characteristics useful for phytoremediation, including vigorous growth, the production of large numbers of seeds, and an ability to grow in poor habitats. Salvador *et al.* (2004) wrote that Amaranthaeae members as weeds in Brazil have the ability to adapt to environmental adversities such as salinity, soil pH, herbicides, altitude, and pollution in different natural habitats. Members such as *Alternanthera philoxeroides* Griseb., *Blutaparon portulacoides* (A. St.-Hil.) Mears, and *Gomphrena globosa* L. can accumulate heavy metals. Indeed, because of such characteristics, some species can be used as bio-indicators of environmental pollution and hence as an important tool in bioremediation. Chinmayee *et al.* (2012) noted that Amaranthaceae species are potential agents of heavy metal accumulation and translocation, which makes them useful in phytoremediation. Bigaliev *et al.* (2003) and Mellem (2008) identified *Gomphrena globosa* and *Celosia argentea* as metal accumulators. It is therefore suggested that detailed studied be conducted to evaluate the potential of these weed species in phytoremediation for decontamination of polluted soils.

CONCLUSION

The present study shows that all three weed species reproduce exclusively by seed and form pure stands or mixed populations. *Allmania nodiflora* and *D. muricata* are hermaphroditic and exhibit autonomous selfing, while *C. argentea* var. *margaritacea* is gynodioecious and avoids autonomous selfing in bisexual flowers. However, the flowers in all three species have adaptations for pollination by wind, insects, and rain water. *Allmania nodiflora* and *C. argentea* var. *margaritacea* produce fruits which dehisce by means of a circumscissile lid to disperse seeds, while *D. muricata* produces indehiscent fruits. All three species are anemochorous, but *A. nodiflora* is also myrmecochorous. The structural and functional characters of flowers are adapted for fruit and seed set achieved with the aid of biotic and abiotic agents; fruits and seeds are also adapted for long-distance dispersal through anemochory and/or myrmecochory in order to colonise both agricultural and non-agricultural areas. These reproductive abilities enable them to expand their distribution range and become widespread weeds.

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Botanica SERBICA

REZIME

Reproduktivna ekologija vrsta *Allmania nodiflora, Celosia argentea* var. *margaritacea*, i *Digera muricata* (Amaranthaceae)

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Allmania nodiflora, Celosia argentea var. *margaritacea*, i *Digera muricata* su jednogodišnje zeljaste korovske vrste koje se razmnožavaju isključivo semenom. Biljke se pojavljuju u junu, a cvetaju u period avgust-februar na poljoprivrednim površinama, odnosno u period avgust-oktobar/novembar na drugim tipovima staništa. *Allmania nodiflora* je funkcionalno hermafroditna. *Digera muricata* je delimično hermafroditna, jer je centralni cvet u trocvetnoj cvasti fertilan, dok su lateralni cvetovi sterilni. *Celosia argentea* var. *margaritacea* je funkcionalno ginodiecna. Kod *A. nodiflora* i *D. muricata*, cvetovi olaksavaju autonomno samooprašivanje kroz sinhronost u sazrevanju muškog i ženskog pola. Kod *C. argentea* var. *margaritacea* takođe postoji olakšavanje samooprašivanja, ali je ono onemogućeno jakom protandrijom. Sve tri vrste su anemofilne i entomofilne. *Allmania nodiflora* i *D. muricata* produkuju plod sa jednim, a *C. argentea* var. *margaritacea* sa više semena. Plodovi *Allmania nodiflora* i *C. argentea* var. *margaritacea* se otvaraju pucanjem poklopca pri čemu se disperguju semenea, dok *D. muricata* produkuje nepucajuće plodove. Sve tri vrste su anemohorne, dok je *A. nodiflora* i mirmekohorna.

Ključne reči: anemohorija, anemofilija, entomofilija, ginodiecija, hermafroditizam, hidrohorija, mirmekohorija