

Pollination ecology and fruiting behaviour in a monoecious species, *Jatropha curcas* L. (Euphorbiaceae)

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***Jatropha curcas* is a pantropical shrub. It is monoecious and protandrous. The ratio of male to female flowers is 29 : 1. Both flower sexes open synchronously. The sexual system facilitates geitonogamy and xenogamy. The flower visitors include bees, ants, thrips and flies; bees and flies effect geitonogamy and xenogamy, while ants and thrips effect only geitonogamy. The fruiting behaviour indicates that the plant might selectively eliminate the growing offspring, especially geitonogamous fruit to allocate the resources available to the plant, mostly for xenogamous fruit. The ability to self-pollinate through geitonogamy is considered to be adaptive for *J. curcas* for colonization.**

MONOECISM, the production of separate male and female flowers on the same plant, is relatively a common sexual system among flowering plants. It is widely prevalent in the members of Euphorbiaceae. Bullock¹ reported monoecy in the members of *Euphorbia*, *Phyllanthus*, *Argythamnia*, *Chamaesyce*, *Cnidioscolus* and *Croton*, and dioecy in *Jatropha* species. Studies made on the pollination ecology of some Euphorbiaceae species in Visakhapatnam region show that *Cicca acida*, *Embllica officinalis*², *Croton bonplandianum*³, *Jatropha gossypifolia*⁴ are monoecious, and *Phyllanthus pinnatus* is dioecious³. The studies also report that *Jatropha* is insect-pollinated, *Croton* and *Phyllanthus* are wind- and insect-pollinated, *Cicca* and *Embllica* are exclusively wind-pollinated. Subba Reddi *et al.*⁵ documented that *Euphorbia antiquorum* and *E. tortilis* are temporally dioecious and insect-pollinated. Subba Reddi *et al.*⁶ reported that *Chrozophora rotteri* is monoecious and beetle-pollinated. According to Cruden⁷, temporal dioecy is to be expected in monoecious species because the flowering sequence within a single inflorescence assures temporal separation of sexual function. Also, this sexual system shows a bias in favour of protogyny. Similarly, protogyny is found to be associated with monoecy in all the species mentioned above except the dioecious species *P. pinnatus*.

Jatropha curcas L. is monoecious with protandry. The details of flowering phenology, sexual system, pollinators and fruiting behaviour are provided and discussed in the light of the above reports.

J. curcas L. (Euphorbiaceae) occurs in the plains and ghats of Visakhapatnam. It is used locally as a hedge plant and also as fencing for agricultural fields. Its populations occurring wild in the Eastern Ghats at an altitude of 900 m were used for the study. Ten populations, one each from a different location (Araku, Paderu, Chintapalli, Chinnagadda, Tajangi, Lammasingi, Lotugedda, Vantlamamidi, Minumuluru and Downuru), were selected for the study. The plant was observed with regard to its flowering phenology, intrafloral functional events and sexual behaviour. The plant produces unisexual flowers, and on this basis, male/female flower ratio was calculated from the daily anthesis records. The floral characters for male and female flowers were separately studied. Thirty undehisced, mature anthers from ten different plants immersed separately in a drop of lactophenol aniline-blue on a glass slide were macerated and observed under the microscope, and the number of pollen grains per anther was counted separately for both the lower tier and the upper tier of stamens. Based on this, the total pollen production per lower tier and per upper tier of stamens was estimated separately by multiplying the number of pollen grains per anther by the number of stamens of each tier. Finally, the total pollen production per flower was calculated. The pollen/ovule (P/O) ratio was determined by dividing the estimate of the number of pollen grains per male flower by the number of ovules per female flower. The ratio of male to female flowers was used to estimate the P/O ratio. The fruiting behaviour was carefully examined according to Aluri and Rao⁸. The breeding system by geitonogamy and xenogamy was tested through hand-pollinations. The geitonogamy was tested by pollinating the female flowers with the pollen of male flowers of the same plant and xenogamy by pollinating the female flowers with the pollen of male flowers from a different conspecific plant. Seventy-eight female flowers, six each from thirteen plants were used for geitonogamy and one hundred and four female flowers, eight each from thirteen plants for xenogamy. Insect foragers were collected and identified. The daily foraging schedules, forage collected, percentage of foraging visits and probing behaviour versus pollination were recorded according to Aluri⁹.

J. curcas is a perennial, deciduous shrub or treelet. It flowers during the rainy season with concentrated flowering from late July to late October. The plant produces flowers in racemose inflorescences, with dichasial cyme pattern. The flowers are unisexual, and male and female flowers are produced in the same inflorescence. Normally, the inflorescences produce a central female flower surrounded by a group of male flowers. In a few, the places where female flowers are expected are substituted by male flowers. Numerically, 1–5 female flowers and 25–93 male flowers are produced per inflorescence. The average male to female flower ratio is 29 : 1. Each inflorescence, once it begins flowering, flowers daily, and the flowering lasts for 11 days (Figure 1). The flowering

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pattern showed that the males flower first and produce flowers daily until the male buds are exhausted. The female flowers bloom between the second and the sixth day.

Male flowers are small, odourless and salver-shaped. Sepals and petals are five each, free; the latter are connivent at the flower base, forming a short tube. Stamens are ten, diadelphous, arranged in two tiers of five each. The lower tier is free, while the upper tier is united. The anthers are yellow, ditheous and dorsifixed. Oval-shaped glands, five in number, are present at the villose flower base. The flowers open daily during 0530–0630 h. The anthers dehisce an hour later by longitudinal slits. The pollen production in the lower tier of stamens is 220, while that in the upper tier of stamens is 435. The total pollen production per flower is 655. The P/O ratio is 6332 : 1. The pollen grains are yellow, globular, inaperturate; the exine is semitectate and verrucate. They are 89 μm in size in the lower tier of stamens and 81 μm in the upper tier of stamens. The floral base contains nectar in trace amount, which is 0.3 μl per flower. The nectar glistens against sunlight. The flowers drop off, mostly on the third day.

Female flowers are quite similar to the male flowers in shape, but are relatively larger. Sepals and petals are relatively larger, the latter form a small tube at the flower base. The styles and stigmas are three each, and the latter are bifid. The ovary has three carpels, each with a single locule producing one ovule. The floral base is villose and contains five yellow elliptical glands under the ovary. The flowers open in synchrony with male flowers. The stigmas are receptive after the flowers open and remain so for three days. The villous flower base secretes nectar in trace amount, which is almost the same in quantity as in male flowers. The unpollinated flowers fall off on the fourth day, while the pollinated ones remain in place; the sepals and petals gradually enlarge and protect the growing fruit until the latter reaches its full size.

Hand-pollination tests indicated 96% fruit set through xenogamy and 77% fruit set through geitonogamy. All xenogamous fruits once initiated develop to maturity; while 23% of the developing geitonogamous fruits abort subsequently, the remaining percentage of fruits develop to maturity. The natural fruit set rate found in selected inflorescences on distantly-spaced plants varied from 37 to 61%. The female flowers in these inflorescences are 351 out of which 177 produced fruit; the fruit set rate

being 50% (Figure 2). In the remaining flowers, some pollinated flowers initially developed fruits but later aborted. Individual fruits begin development immediately following fertilization. Fruits grow to full size over a two-month period, with concentrated growth in the third to fifth week. The fruits are green first, later yellow and finally brown/black. The matured fruits dehisce passively and seeds fall off together with the capsule.

The flower-visitors included bees, ants, thrips and flies (Table 1). They foraged daily during daylight hours from 0730 to 1800 h. They foraged on male and female flowers indiscriminately and made relatively more visits on male flowers. On male flowers, bees made 64% of their total visits, flies 55% and ants 56%, while on female flowers, bees made 36%, flies 45% and ants 44% (Figure 3). Of the total foraging visits made by insects on male flowers, bees contributed 34%, ants 61% and flies 5%, while on female flowers, bees made 28%, ants 70% and flies 2% (Figure 4). All the insect species recorded were found foraging throughout the flowering period.

Bees and thrips collected nectar and pollen from male flowers mostly in the same visit, and nectar from female flowers. Ants and flies collected only nectar from both male and female flowers. The bees probed the flowers in an upright position, by landing on the petals and stamens in male flowers and on the petals, styles and stigmas in female flowers. They collected pollen from the dehisced anthers of both the upper and lower tier of stamens. In doing so, their ventral side was coated with pollen and part of it was groomed later by them and loaded into their corbiculae. The bees also collected nectar from the flower base. When they visited female flowers for nectar collection, their pollen-laden ventral side brushed against the stigmas and effected pollination. The bees mostly collected floral rewards on different conspecific plants, effecting geitonogamous and xenogamous pollinations. Thrips, because of their tiny size, freely moved in the flowers and gathered both floral rewards. They stayed on the same plant all the time, effecting geitonogamy. Ants and flies foraged on the flowers in the manner that the bees did, the former confined to the same plant thus effecting geitonogamy, while the latter foraged on different conspecifics, effecting geitonogamy and xenogamy. The large-bodied ants, *Camponotus* spp. carried pollen on their ventral side while the small-bodied ants, *Cre-*

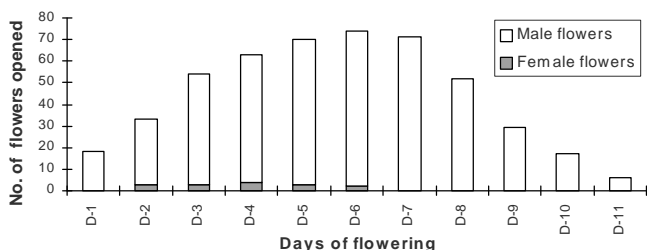


Figure 1. Flowering phenology in *J. curcas*.

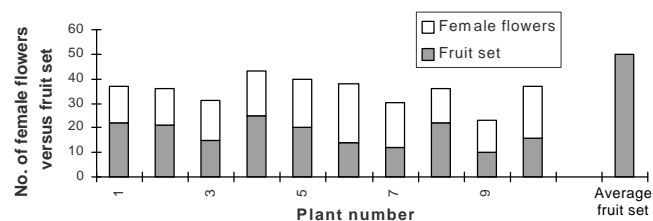
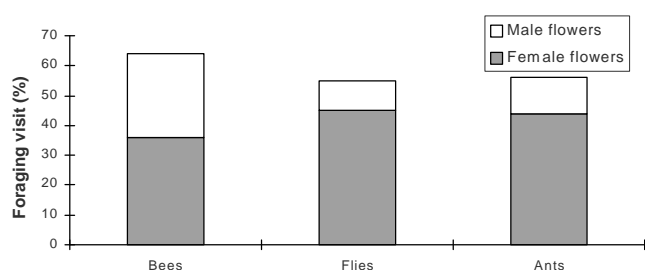
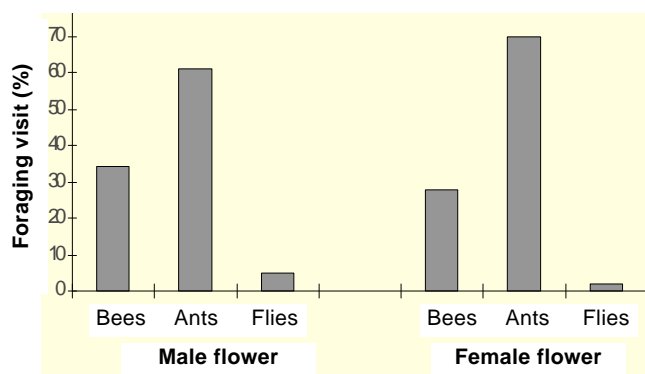


Figure 2. Fruiting behaviour in female flowers of *J. curcas*.

Table 1. List of flower visitors and forage collected by them on *J. curcas*

Order	Family	Genus	Species		
Hymenoptera	Apidae	<i>Apis</i>	<i>florea</i>	Nectar and pollen	
			<i>indica</i>	Nectar and pollen	
	Anthophoridae	<i>Trigona</i>	<i>iridipennis</i>	Nectar and pollen	
			<i>simillima</i>	Nectar and pollen	
	Halictidae	Unidentified		Nectar and pollen	
	Formicidae	<i>Camponotus</i>	<i>compressus</i>	Nectar	
			sp.	Nectar	
			<i>Crematogaster</i>	sp.	Nectar
			<i>Solenopsis</i>	<i>geminata</i>	Nectar
			<i>Pheidole</i>	<i>spathifer</i>	Nectar
Thysanoptera	Thripidae	<i>Scirothrips</i>	<i>dorsalis</i>	Nectar and pollen	
		<i>Thrips</i>	<i>hawaiiensis</i>	Nectar and pollen	
		<i>Chrysomya</i>	<i>megacephala</i>	Nectar	

**Figure 3.** Relative percentage of foraging visits made on male and female flowers of *J. curcas*.**Figure 4.** Relative percentage of foraging visits of insects on *J. curcas*.

matogaster, *Pheidole* and *Solenopsis* carried pollen on both ventral and dorsal sides. On a daily basis, the female flowers occur in a small number at plant and population levels, and usually receive sufficient amount of pollen deposits, ensuring pollination.

According to Cruden⁷, temporal dioecism is to be expected in monoecious families. *E. antiquorum* and *E. tortilis* are monoecious and exhibit temporal dioecism because the flowering sequence within single inflorescences assures temporal separation of sexual function⁵. Bullock¹ reported that *Euphorbia*, *Phyllanthus*, *Argythamnia*, *Chamaesyce*, *Cnidocolus* and *Croton* in Mexico are monoecious, but he had not mentioned whether temporal dioecism in these genera exists or not. Temporal dioecism has not been reported in the monoecious

species, *C. acida*, *E. officinalis*², *C. bonplandianum*³, *J. gossypifolia*⁴, and *C. rotleri*⁶. These studies indicate that temporal dioecism need not be expected in the monoecious species. In the present study also, *J. curcas*, although clearly exhibits monoecy, does not indicate temporal dioecism. Further, the studies mentioned above documented that protogyny is associated with monoecy. On the contrary, *J. curcas* shows protandry by opening male flowers on the first day. The flowering sequence indicates that female flowers open from the second day to the sixth day, while male flowers open from the first to the last day of flowering at inflorescence level. Although *J. curcas* exhibits protandry, it is weak and appears to have no appreciable role to minimize geitonogamy and promote xenogamy. Further, the plant produces male flowers where female flowers are expected, and also produces only male flowers in a few inflorescences on some individuals. It is not clear whether this represents polygamy or marked dichogamy. Such a flowering pattern has been evidenced in some *Argythamnia* species¹. The flowering sequence of male and female flowers in *J. curcas* facilitates geitonogamy and xenogamy. The high natural fruit set recorded indicates that the plant is capable of producing fruit through geitonogamy and xenogamy. Such a breeding system represents facultative xenogamy. Cruden¹⁰ predicted that P/O ratios are the indicators of breeding systems. The P/O ratio found in *J. curcas* is more than that predicted for facultative xenogamy. The high P/O ratio seems to be imperative to compensate the pollen loss associated with the pollen-collecting behaviour of bees and thrips. By predominantly cross-pollinating, the plant throws open the possibilities for geitonogamy. In line with this, the plant might be selectively eliminating the growing offspring, especially those originated from geitonogamy, in order to allocate resources for the xenogamous fruits. The facultative xenogamous breeding system is adaptive for colonizing species like *J. curcas*¹¹, as it facilitates fruit set through geitonogamy with the resident flower-visitors like ants and thrips on the plant, in the absence of xenogamy which requires inter-plant flower visitors. Therefore, such a

breeding system is required for *J. curcas* to occupy different habitats and build up its own populations.

The shallow, light and simple flowers, providing a platform are shown to be characteristic of fly-pollinated flowers¹². These characters are found in *J. curcas*. The flowers provide easy access to the foragers. They produce copious amount of pollen at inflorescence level. The pollen placed in two tiers of stamens, advertises its existence. Further, nectar secreted in traces at the shallow flower base glitters against sunlight and advertises its existence to the foragers. Usually, nectar is concealed and does not advertise its existence¹³.

The individual flowers are grouped together in the racemose inflorescences, an arrangement which promotes attraction and foraging rate by the foragers. The plant with monoecious sexual system essentially requires an agent for pollen transfer from male to female flowers, within or between conspecific plants. The floral rewards in both flower sexes are accessible even to short-tongued anthophilous insects. The bees, by collecting pollen and nectar and by moving between male and female flowers within and on different conspecific plants, effect pollination in a messy and soiled manner¹². The flies also exhibit the same foraging behaviour and effect pollination. Ants and thrips remain on the same plant and effect geitonogamy only. Although all insect species effect pollination, only bees and flies effect xenogamy. The flies are represented by only one species, *Chrysomya*, and they are under-represented among the pollinators. They generally utilize many different sources of food, and usually their pollinator activity is unreliable. The proximity of a suitable breeding ground, frequent wet, decaying vegetable and dung material is important for their presence in the vicinity of *J. curcas*. In the study areas the decaying, wet material or dung or fallen decaying fruits are not found. Hence the absence of flies, especially small-bodied *Musca*, *Eristalis*, etc., which have small-distance flight range, is not surprising. The introduction of breeding material in the vicinity of *J. curcas* allows the flies to utilize the same for breeding and the flowers for food, while effecting pollination.

The natural fruit set rate indicates that the plant does not suffer seriously from under-pollination. The production of female flowers in small number, surrounded by a large number of male flowers in *J. curcas* seems to be a strategy to ensure pollination to the maximum extent. The stigma receptivity lasting three days also additionally provides opportunities for pollination, if not pollinated on the first and second day. The study indicates that pollen is deposited in sufficient amount, which is visible by its yellow colour even to the naked eye. However, the plant with predominant xenogamy requires mostly xenogamous pollen for more fruit set, after selective elimination of growing fruit. Therefore, pollen transfer between conspecifics has a great bearing on the net percentage of natural fruit set.

1. Bullock, S. H., *Biotropica*, 1985, **17**, 287–301.
2. Subba Reddi, C. and Reddi, E. U. B., *Proc. Indian Natl. Sci. Acad. Part B*, 1984, **50**, 66–80.
3. Reddi, E. U. B. and Subba Reddi, C., *ibid.*, 1985, **51**, 468–482.
4. Reddi, E. U. B. and Subba Reddi, C., *Proc. Indian Acad. Sci.*, 1983, **92**, 215–231.
5. Subba Reddi, C., Aluri, R. J. S. and Bahadur, B., *J. Palynol.*, 1995, **31**, 291–300.
6. Subba Reddi, C., Aluri, R. J. S. and Veerabhadraiah, G., *ibid.*, 1998, **34**, 151–156.
7. Cruden, R. W., *Bot. Gaz.*, 1988, **149**, 1–15.
8. Aluri, R. J. S. and Rao, S. P., *Curr. Sci.*, 2002, **82**, 1466–1471.
9. Aluri, R. J. S., *Plant Sp. Biol.*, 1989, **4**, 107–116.
10. Cruden, R. W., *Ann. Mo. Bot. Gard.*, 1976, **63**, 277–289.
11. Baker, H. G., *Evolution*, 1967, **21**, 853–856.
12. Faegri, K. and Pijl, L. van der, *The Principles of Pollination Ecology*, Pergamon Press, Oxford, 1979.
13. Kumar, H. D., *Plant-Animal Interactions*, Affiliated East-West Press, New Delhi, 2000.

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Onset of climate change at Last Glacial–Holocene transition: Role of the tropical Pacific

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We study palaeoclimatic records from various sites spread around the earth, focusing on the start of the last glacial–interglacial transition. The warming, as recorded in the $d^{18}\text{O}$ record started first in the tropics, then propagated to the Antarctic and then finally to the Arctic. Our analysis of the data suggests that it took about 7.6 ka for onset of climate change to propagate globally. We propose that the tropical Pacific played a major role in initiating the warming in the tropics. We discuss mechanisms that could have transported this heat from the tropics to Antarctica and then to the Arctic during transition to the interglacial.

NUMEROUS polar and tropical ice cores, marine cores and continental records indicate that the climate has changed significantly over the past hundreds of kiloyears. Many

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