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The Floral Biology of *Jatropha curcas* L.—A Review

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Abstract *Jatropha curcas* L. (Euphorbiaceae) has attracted considerable recent attention as a potential horticultural crop based on the quality of its oil seed for biodiesel production, and its ability to grow in unproductive subtropical or sub-desert soils. Additionally, several characteristics of the species make it a good model for a more thorough understanding of the reproductive biology of a species undergoing the domestication process. To date, there is limited information about its reproductive patterns and the genetics involved. Such information is necessary for developing efficient agronomic practices and for guiding the research needed to more fully understand the species' reproduction processes. *J. curcas* has an inconsistent mating system, which presents both opportunities and challenges in developing breeding strategies and agronomic practices. Unraveling the mating system of *J. curcas* can increase our understanding of the evolution of reproduction systems in monoecious plants. The influences of environmental factors on flowering and floral organ development have not been reported under either field or controlled conditions. Moreover, no genetic mechanisms controlling the characteristics of the flowering (architecture, sex expression and sex ratios) have been proposed. The present review assesses and synthesizes the current knowledge of the floral biology of *J. curcas*. It provides a description of the species, its reproductive organs and reproductive patterns, and discussing the factors influencing them.

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Background

The genus *Jatropha* (Euphorbiaceae) is widely distributed throughout the tropics and subtropics in two big groups, the Jatrophas of the Old World (Asia and Africa) and the Jatrophas of the New World (the Americas) (Dehgan and Webster, 1979). However, the phylogenetic and genetic relationships are not known for most of the species in the native range of *J. curcas*. The traits shared by the relatives of *J. curcas*, as well as the derivations from hybridization at the intrageneric level, have received little attention. Such studies may facilitate the understanding of several features of the reproductive patterns of a species being introduced to agricultural production.

Jatropha curcas L. is native to the tropical and subtropical regions of Mexico and Central America. However, according to Carels (2009) and in response to E. W. Berry's observations (1929 cited by Carels, 2009), the most accurate determination of the origin of the *J. curcas* is tropical South America. Currently, the natural area of distribution of *J. curcas* corresponds to tropical climates, which—according to Köppen (1948, cited by Maes et al. 2009)—correspond to tropical monsoon and savanna climates. The tropical monsoon climate (denominated as A_m in the Köppen's classification) results from a seasonally reversing wind accompanied by corresponding changes in precipitation; this climate has a driest month with rainfall less than 60 mm, usually the month closest to the winter solstice. The savanna climate (A_w) has a pronounced dry season, with the driest month receiving precipitation less than 60 mm. *J. curcas* also occurs in temperate climates without an intensive dry season, such as the humid subtropical climate (C_{fa}), in which the coldest month's mean temperature is between −3 °C and 18 °C, and the warmest month's is above 22 °C, with no distinguishable dry season. *J. curcas* is not commonly present in semiarid or arid climates, such as steppe climate (B_s) in which the precipitation is less than the potential evapotranspiration, or hot semi-arid climate (B_w) which tends to have hot, sometimes extremely hot, summers and mild to warm winters, a climate common in the tropics and subtropics. In Mexico, natural and cultivated areas of distribution are near tropical or subtropical zones with high humidity, sometimes with a dry season that lasts no longer than three months.

J. curcas has attracted attention for its potential as a biofuel crop and its growth in unproductive subtropical and subdesert soils (King et al. 2009). The oil from its seeds possess nearly equal proportions of oleic (~45 %) and linoleic (~33 %) acids, and contains saturated fatty acids such as palmitic and stearic. In addition, the oil has the necessary physical characteristics (viscosity and density) appropriate for a biodiesel fuel (Akbar et al. 2009). Despite these desirable biofuel properties and crop production potential for the species, constraints on the species as a biofuel crop arise due to a lack of knowledge about its reproductive patterns and how to control flowering for maximum productivity. Several plant characteristics, such as self-compatibility, a short juvenile period, a diploid small genome (with the possibility of producing artificial triploids and tetraploids, polyploid relatives, the availability of molecular markers, and protocols for tissue culture transformation and regeneration, make *J. curcas* a model for studies of flowering expression in monoecious trees. Monoecious plants are species possessing distinct (separate) male and female structures in the same plant, but in separated flowers (either within the same inflorescence or not).

A wide range of studies need to be done on *J. curcas*, from molecular and biochemical to genetic, environmental, ecological, and even its economic and social impacts. However, to date, most attention has been focused on the establishment of areas for production, leaving basic research in second place. Additional research is needed to successfully exploit the species.

The present review attempts to assess and synthesize current knowledge on the floral biology of *J. curcas*. It provides a general description of the species and a comprehensive description of its reproductive organs and mating system. Subsequently, genetic and environmental factors influencing reproduction of the species are reviewed. Finally, conclusions and remarks are provided.

The Plant

J. curcas is a tree, up to 5 m in height, with thick branches containing whitish latex. The trunk has grey to reddish bark. The arrangement of the leaves on the steam (phyllotaxis) is alternate to subopposite, similar to a spiral, and the leaf shape is palmate, with three to five lobes. The flowers are disposed in clusters containing both female and male flowers at the apex of the branches. Flowering in *J. curcas* is continuous. Fruits, which are located at the base and medium sections of the branch, can be seen at different ripening stages while flowers are present at the top (Carels, 2009). The fruit is trilocular with an ellipsoidal shape; its color depends of the stage of maturity, progressing from green to yellow to brown. The exocarp is fleshy before the seeds mature. The seeds are blackand rich in fatty acids and other chemical compounds such as curcin (a ribosome-Inactivating protein of type N-glycosidase, considered phytotoxic in *Jatropha* species) and esters of phorbol [a diterpene compound, which in some forms can act as tumor promoters and stimulators of cytokine production]. Phorbol was found first in *Croton*, another Euphorbiaceae species. *J. curcas* roots can extend beyond the tree crown width and to depths of 1.20 m in plants grown from seed. The roots distribute heterogeneously in the soil, with most of the lateral roots located in the topsoil layer.

J. curcas is considered a perennial crop exhibiting paradormancy, which implies that the plants exhibit suppression of growth and development to conserve energy and ensure survival during adverse environmental conditions. The slowdown of tree growth precedes winter or seasons of extreme conditions, such as absence of rainfall which may be accompanied by extreme oscillations in temperature.

Some *J. curcas* accessions show precocity and undergo a short juvenile stage. From the author's observations, 5-month-old seedlings planted 30 days after germination on the south coast of California (in June) came to flowering in less than 1 year (October). However, stabilization of yield under agro-management occurs only after the third year. Irregular flowering and yield are also common in plants before the third year. In fact, Heller (1996) reports several contradictory observations about the flowering patterns and seed yields worldwide for the first seed harvest, as well as difficulties in predicting a planting's real yield potential. The limited information available for the species' agronomic handling is a serious constraint to large-scale exploitation (Divakara et al. 2010). Successful production of *J. curcas* requires much more basic knowledge of its agronomic traits.

Dehgan and Webster (1979) considered *J. curcas* to be a monoecious plant; however, it sometimes produces hermaphrodite flowers. This sexual expression is described as "polygamonoecious" or "trimonoecious" by Sakai and Weller (1999). Raju and Ezradanam (2002) observe that, in addition to monoecism, *J. curcas* expresses protandry (i.e. pollen is shed before the ovules are mature), because 60 % of the female flowers open between the third and fifth day after the opening of the first male flower.

Given the above reproductive patterns and the capacity of *J. curcas* to hybridize with other species of the genus, Dehgan and Webster (1979) considered *J. curcas* to be the most basal lineage in the genus. Its haploid chromosomal number is $n=11$. *J. curcas* has a genome of only 416 MB (similar in size to those of rice and *Ricinus communis* L.) with a GC composition of 38 % (Carvalho et al. 2008), which corresponds to that typically found in core dicots (Carels, 2005, cited by Carels, 2009). The chloroplast DNA (cpDNA) of *J. curcas* is a circular molecule 163,856 bp in length, containing 110 distinct genes [78 of which code for proteins, 4 for ribosomal RNA (rRNA), and 28 for distinct forms of transfer RNA (tRNA)] (Asif et al. 2010). In addition, genome organization and arrangement are similar to those reported for angiosperm chloroplasts, with the exception that *J. curcas* has lost the *rps16* and *infA* genes, which are often tracked to study land plant evolution and species divergence in the plant kingdom. Phylogenetic analyses have shown that *J. curcas* is strongly related to the genus *Manihot*. *J. curcas* also shares many features with *Populus* and *Passiflora* and, in a minor way, with *Cucumis*. All of these genera are members of the Eurosids clade (Asif et al. 2010). Sato et al. (2011) report that, at the microsyntenic level, *J. curcas* is highly related to *R. communis* (53 % similarity), and that genetic flowering regulators from *J. curcas* are closely related to those in *Betula pendula* L., *Hevea brasiliensis* L. and *Vitis vinifera* L.

Flowers and Inflorescence

J. curcas bears its flowers disposed in racemose inflorescences (Fig. 1a) in a dichasial cyme pattern (called diclin inflorescences), in which distinct coflorescences are common (Carels, 2009). These inflorescences are distributed over the entire canopy, with higher concentrations observed in areas having greater exposure to light. The following descriptions of the inflorescences and flowers of *J. curcas* are based mainly on those of Burger and Huft (1995), complemented by the author's observations and related information from various authors.

Inflorescences are solitary, varying from 5 to 25 cm in length and are borne terminally or axillary. They are commonly bisexual (with flowers of both sexes), but may be unisexual. The peduncles are glabrous or puberulent, and range from 1.5 to 10 cm in length, with thickness ranges from 0.8 to 2 mm. Bracts present on the inflorescences are lanceolate without marginal glands, 2–15 mm in length, and their distal axes are puberulent. Between 10 and 20 % of the flowers in an inflorescence are female and around 8.6 % of the inflorescences are exclusively male. These percentages vary from plant to plant, and population to population, in response to time, climate, and nutrition (Luo et al. 2007). Five to nine sub-branches of dichasium are produced, which include female flowers at the first joint of the dichotomous branching. Commonly a female flower is on the top (Fig. 1b), while the first sub-branch may produce female flowers at the second joint of dichotomous branching (Luo et al. 2007). The top flowers in the inflorescence are commonly the first to open; subsequently, the male flowers (Fig. 1c) open at the branch joint, followed by the female flowers.

According to Liu et al. (2008), the first sepal primordium is initiated in the non-median abaxial position and the

Fig. 1 Inflorescense and flowers of *J. curcas*. **a** typical young inflorescence; the flower with large scales at the top will be a female flower. **b** opened female flower in the middle of a group of male flowers. **c** just open male flower; the light yellow items on the anthers are cumulus of pollen grains. **d** diadelphous stamens with some pollen grains

second in the median adaxial position during floral organogenesis of three *Jatropha* species (*J. curcas* is among them). Five sepal primordia arise in a 2/5 sequence on the periphery of the floral apex, initiated either anticlockwise or clockwise in different floral buds of the same species. The five petal primordia initiate simultaneously. In the male flower, the five stamen primordia of the outer whorl arise simultaneously, and then five of the inner whorl initiate simultaneously. In the female flowers, three carpel primordia appear simultaneously; then the ovary bulges and the stamens degenerate, whereas in the male flowers, the stamens grow normally but the ovary is absent.

Wu et al. (2011) propose a 12-phase division of the development of the organs of *J. curcas* flowers. During the first six phases, the female flowers present bisexual tissues. Abortion of the male structures occurs during the seventh phase, beginning sexual differentiation. Conversely, male flowers exhibit male tissues throughout development. The male flowers are greenish yellow, on pedicels 1 to 5 mm in length, which are articulated just below the flowers (Luo et al. 2007). The sepals are oblong to obovate, 2.8–4.5 mm in length, and 1.3–1.8 mm in width, without reflex, with a rounded apex, and are broadly imbricate when in bud. The petals are reflexed and connivent at their base (Luo et al. 2007), and range from 5 to 7.5 mm in length. Petal lobes are obovate to oblong. Usually, sepals and petals are both five and free (Luo et al. 2007). The stamens range from 2 to 7 mm in length. The stamens are diadelphous (i.e. they are fused together at least partly by the filaments so that they form two separate bundles, or a bundle plus a lone separate stamen) in two tiers of four or five each. Luo et al. (2007) mention that the outer tier of stamens is free, while the inner tier is united. The stamens are dicyclic, (occur in two whirls) with the outer whorl opposite to the petals (obdiplostemony) and the inner whorl opposite to the sepals (Liu et al. 2007). Each stamen bears four microsporangia arranged in two thecae (Liu et al. 2007). The 10 anther lengths range from 1 to 2.2 mm and commonly stand higher than the reflexed sepals. Anthers are dithecous, dorsifixed, and dehisce by longitudinal slits. They have a predominantly yellow color, and emerge over the course of 2 days (Luo et al. 2007). Pubescence covers the floral disc with five oval-shaped yellow glands 0.03 mm long and 0.02 mm wide. The pistilloide is absent. Luo et al. (2007) consider the life span of the male flowers to be around 2 days.

The female flower does not over all differ from the male flower, being similar in color and fragrance (which is slight in both) (Luo et al. 2007). The female flowers are on pedicels 5–9 mm long. The sepals do not attach to the petals; the sepal length is around 3.7–6 mm long without fusing at the base. The sepals' shape is diamond-like, and they do not roll reversely, (Luo et al. 2007). The sepal lobes, ca. 2.5 mm wide, are oblong to lanceolate and the apex is obtuse to subacute, The petals are approximately 7 mm long, and are not fused at the base, but possess reversal rolling, resulting in being arranged like imbrications that form a small tubular structure at the base (Luo et al. 2007). The ovary is glabrous, ca. 2.5×2 mm, with stylar columns 0.5 mm and style branches 1.5 to 2 mm in length. The ovary typically comprises three ovules. The styles and stigmas are both three. The stigmas are bifid, and are a darker green than the petals and ovary (Luo et al. 2007). The floral base is villose, containing five flat square yellow glands 0.02 mm in length (Luo et al. 2007). Yellowish honeydew is frequently seen clearly at the flower base. The female flowers often emerge for 5–8 days although Luo et al. (2007) reported a female flower life span between 5 and 12 days. According to Ashoke et al. (2005), the stigmas become receptive between 1 and 2 h after the flower opens. During stigma receptivity, the lobes are open and exhibit a green coloration; additionally, the surface area increases to approx. 1.62 mm in diameter and coincides with nectar secretion. Stigma receptivity declines after the 5th day and is lost by the 9th (Divakara et al. 2010). Nair and Abraham (1962) report ten staminoides in two whorls. These staminoides, in addition to the occasional presence of hermaphroditic flowers, support the observation that unisexuality of the flowers is secondary to a previous bisexual stage during the female flower development of *J. curcas*.

Hermaphroditic flowers, although considered rare (only 0.005 %), have been reported by several authors (Dehgan and Webster, 1979; Liu et al. 2007; Luo et al. 2007; Abdelgadir et al. 2010), and may be considered an abnormality in female flower development (Luo et al. 2007). Hermaphroditic flowers are very similar to the female flower in size, shape, color and arrangement of the female reproductive organs. The main difference is hermaphroditic flowers have 8 to 10 stamens, which are arranged similarly to those in the male flowers.

Luo et al. (2007) observed what they called a "neutral flower", usually terminal, with a shape and size quite similar to those of female flowers. However, the petals were smaller and paler, with the sepals considered as degenerated because they were minuscule. The neutral flower's main characteristic is that "the floral base does not contain a pistil or stamen". Abdelgadir et al. (2010) also reported this kind of flower in plants treated with growth regulators. Neutral flowers can be considered nonfunctional due to their incapability to bear reproductive organs.

The pollen (Fig. 1d) is described by Ashoke et al. (2005) as apolar-radiosymmetric, inaperturated and spheroidal, 94.55 μm in diameter and with a 6.2 μm thick exine (exosporium). Luo et al. (2007) describe the pollen as globular and verrucated, averaging 57 μm in diameter (between 52.5 and 70μm). One flower produces approximately 1700 grains of pollen (Ashoke et al. 2005), although Luo et al.

reported from 1597 to 5763 grains. Whether the differences reported in pollen size and morphology are due to environmental or genetic differences remain unknown. According to Dehgan and Webster (1979), the pollen grains of the genus *Jatropha* are likely binucleate. The pollen from hermaphroditic flowers is weaker in comparison to that from the male flowers (Abdelgadir et al. 2010), displaying lower viability, lower germination rates, and abnormally shaped and shorter pollen tubes when they are grown in vitro (Abdelgadir et al. 2009b, 2012). Luo et al. (2007) found that the pollen maintains viability for between 9 and 33 hours after blooming. It becomes nonviable 48 hours after anthesis. Acharya et al. (2011) report that heavy metals, such as Cd, Cr, Zn, Cu, Hg and Pb, in concentrations above 200 μM may be responsible for low levels of pollen germination and shorter pollen tubes as a result of toxicity. Cd, Zn, Hg and Pb were the metals exerting critical toxic effects. According to Liu et al. (2007), the mature pollen grains in *J. curcas* are both inaperturated and two-celled, and most of the tetrads are tetrahedral, with a few grains being irregularly tetrahedral. Additionally, pollen abortion may take place in one or two microsporangia per anther; although, a low ratio of aborted pollen has been reported in the species (Liu et al. 2007).

In Thailand, Malaipan et al. (2008) report variable pollen germination of *J. curcas* depending on the clone (genotype), the location of the flowers in the canopy with respect to the sun, the time of pollen collection, and the blooming stage. Overall, 30–77 % of the pollen germinated. Highest rates of germination (>65 %) were observed in flowers directly exposed to the sun, at the apex of the plants, collected during the late blooming stage, and located in the third group of blooms on the stem. Additionally, the authors report a flower sex ratio (female:male), of 1:9 in March, decreasing to 1:22 in October. Raju and Ezradanam (2002), Luo et al. (2007), and Abdelgadir et al. (2009c), report sex ratios of 1:29, 1:24.5 and 1:16 respectively; while Ashoke et al. (2005) report sex ratios of 1:20 to 1:108. In addition, changes in the sex ratios have been reported from year to year. According to Prakash (2007, cited by Divakara et al. 2010), a plantation of *J. curcas* presented a 1:25 flower sex ratio the first year, but a 1:13 the second year.

Mating System

The mating pattern (also called the breeding system or mating system), refers to the way a plant reproduces in nature or in a cultivated system. Mating system depends on the movement and availability of opposite gametes in the (agro)ecosystem, the phenotypes and genotypes of the parents, and environmental factors. Panmixis, defined as the random mating in the system, permits inferences about the course of evolution of the plant population, gene flow, genetic drift, genetic structure, and the direction of selection. None of the three mating systems—geitonogamous (self-pollination), xenogamous (outcrossing) and apomictic (setting of seeds without fusion of gametes)—exclude the others during the movement and encounter of opposite gametes of the same plant species.

For the genus *Jatropha*, an autoxenogamous mating system with incidence of polyploidy and diverse growth habits has been suggested (Dehgan and Webster, 1979). *J. curcas* shows dependence on insect pollinators such as *Chrysomya megacephala*, several species of the *Apis* genus, and various species of ants. The availability of appropriate numbers of pollinators in the areas of production is necessary for profitable seed yields (Vaknin 2012). Pollination of *J. curcas* in the wild (Fig. 2a) is influenced by pollen deposition on the stigmas (Fig. 2b) and nectar availability (Ashoke et al. 2005). Since pollen can be dispersed only 4–5 m from the male parental tree (depending on wind velocity, environmental humidity, and natural barriers), pollination by wind is rare (Luo et al. 2007). The maximum pollen flow is only 2.8 pollen grains per cm^2, and the probability of a grain being carried to the stigma (2.06 mm^2) by the wind is almost nil. Abdelgadir et al. (2009c) calculated a pollination limitation index (L) of 0.03. L is an index used to describe when a plant population presents limitation in fruit setting given by limited supply of pollen. In a controlled experiment with individuals of the same species under controlled conditions $L=1-(Po/Ps)$, where Po is the average fruit set percentage in the open-pollinated (control) plants, and Ps is the average fruit set percentage in plants that received additional cross-pollen. A value of $L=0$ indicated no pollen limitation in the population under study. The index has a lower bound of zero because when negative indices are obtained, these likely result from experimental or Type I statistical error, and are not informative.

The number of pollen grains per ovule in *J. curcas* has been determined by Raju and Ezradanam (2002) as 6332, by Ashoke et al. (2005) as 539 and by Luo et al. (2007) as between 13,015 and 46,968. These values can be a useful index for determining the probable mating system (Cruden 1977). However, some of the values given above are higher than those proposed by Cruden. Thus, the mating system is probably that of obligate xenogamy. Additionally, temporal dioecism is not seen in the species, but self-compatibility is observed in 93.2 % of fruit set in the experiments of Luo et al. (2007).

Luo et al. (2007) used the method proposed by Dafni (1992) to classify the breeding system of *J. curcas* as outcrossing, partially self-compatible, and requiring pollinators. Luo and collaborators estimated the outcrossing index for *J. curcas* to be 3 to 4. However, Dhillon et al. (2006, cited by Divakara et al. 2010) believe that cross-pollination is a facultative ability, while Qin et al. (2007, cited by

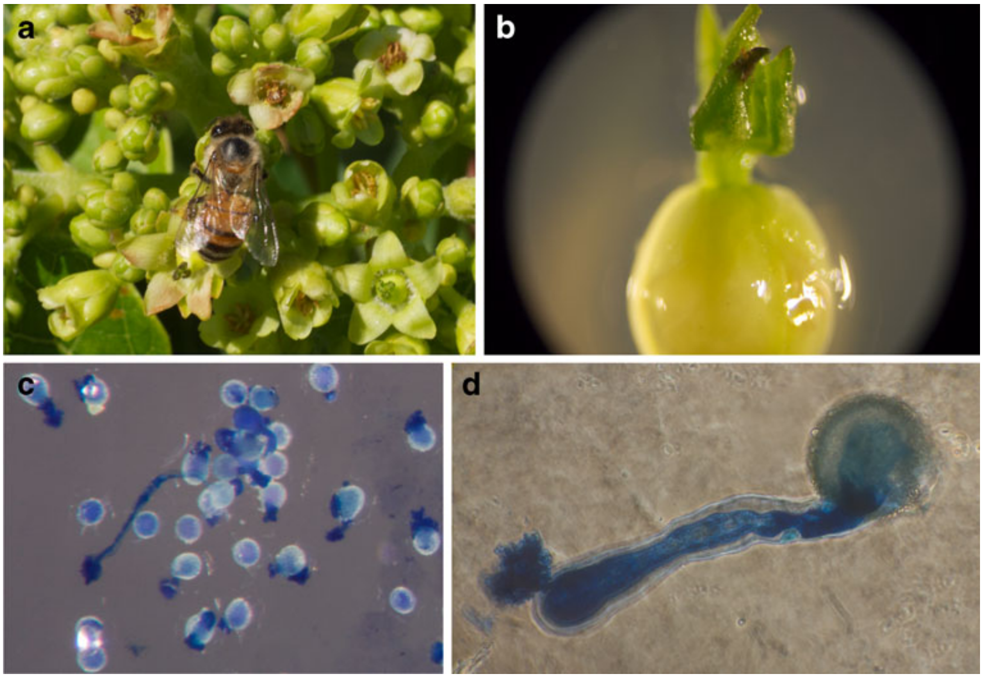

Fig. 2 The pollination of and pollen from *J. curcas*. **a** a bee visiting an inflorescence of *J. curcas* in the southcoast of California. **b** an isolated gynoecium exhibiting the changes in the stigma resulting from pollen deposition (dark zone). **c** germination of fresh pollen grains after 24 h on a gelatinous media; the pollinic tubes were stained with Evan's blue colorant. **d** a 40x picture of a germinated pollen grain of *J. curcas* after 12 h of deposition in a constant growth media

Divakara et al. 2010) consider *J. curcas* as tending towards cross-pollination. Kaur et al. (2011) report a range in fruit setting depending on the mating system; thus cross-pollination resulted in 93.2 % fruit setting, self-pollination resulted in 72.2 % fruit setting, open-pollination resulted in 79.2 % fruit setting, and 36.2 % fruit setting in flowers that were handled in a way to promote apomixis (i.e. flowers emasculated prior to anthesis and subsequently bagged). Raju and Ezradanam (2002) suggested that these multiple matting systems in *J. curcas* are part of an adaptive strategy of species that are good colonizers.

Apomixis is the asexual formation of a seed from the maternal tissues of the ovule, by-passing the processes of meiosis and fertilization, leading to asexual embryo development. The expression of 32 % apomixis has been reported for a small population of *J. curcas* trees (10 trees) by Raju and Ezradanam (2002), with Luo et al. (2007) also suggesting the possibility of apomixis in the species. On the other hand, Ambrosi et al. (2010) performed a study to determine ploidy in several commercial accessions of *J. curcas* and found that 190 seeds out of 2500 possessed embryos with diploid DNA content ($2C$), accompanied by small endosperms with triploid DNA content ($3C$), which discounts the possibility of asexual reproduction by means of gametophytic apomixis. Although Ambrosi et al. (2010) considered the triploid endosperm as evidence of an obligate sexual reproductive system; the occurrence of adventitious embryony remains a possibility. Also, these authors considered the mating pattern in *J. curcas* as tending towards autogamy, based on their analysis of molecular markers (presented in the next section).

The mating system of *J. curcas* may be considered as a facultative mixed system between geitonoamy and xenogamy, with added apomixis and entomophilous pollination. However, the factors leading to one mating system or another are not truly known. This unknown has significant implications on the potential introduction of transgenic *J. curcas* (Gressel, 2008). Information about gene flow in the native range of distribution of *J. curcas* is scarce whether they are in wild, semi-wild, or in cultivated populations. Furthermore, the ratio of gene interchange among other *Jatropha* species has not been evaluated.

A consequence of this mixed mating system is the possibility of latent inbreeding depression in *J. curcas*. Abdelgadir et al. (2009b) estimated inbreeding depression based in the proportion of fruits aborted. They report that 25 % of fruits from self-pollinated flowers aborted before maturation. Additionally, they report that progeny from self-pollinated flowers had weaker roots than did the outcrossed progeny, a pattern similar to that reported in avocado (*Persia americana* L.) as a result of inbreeding depression (Gazit and Degani, 2002). Abdelgadir et al. (2009c) conclude that success in *J. curcas* pollination is not influenced by the mating system, but by differences that can arise as a result of a possible inbreeding depression.

Since the mating system of *J. curcas* can lead to inbreeding depression which is detrimental to yield, breeding strategies to assure outcrossing, such as pollen conservation, are highly desirable. Germination of fresh pollen was 80 % in a gelatinous medium containing sucrose, K, P, Mg, Ca and B took around 20 h in the presence of light, at 30 °C (Fig. 2c and d). In the absence of light, only 57 % of the pollen germinated ($p \leq 0.05$), which suggests that light promotes germination and that the pollen is sensitive to temperature changes and likely also to relative humidity. Germination of pollen from Indian plants growing in a greenhouse at the University of California, Davis, was severely reduced (40 %) when the pollen was stored at 4 °C for 24 h and almost completely eliminated after 60 h of storage (personal unpublished data). Studies in vivo pollen germination on the stigma under controlled environmental conditions are needed to suggest optimal conditions for gametic fusion.

Strategies based on the conservation of pollen at sub-zero temperatures (using N_2 or CO_2) for long-term storage should be investigated to allow for outcrossing and to decrease inbreeding. These strategies would complement breeding programs and avoid inbreeding bottlenecks through germplasm mixing using exotic genetic material from stored pollen (Ganeshan, 1998). In addition, floral synchrony is not required for such an interchange, allowing for hybridization at any desired location. In tropical crops such as cherimoya, the use of pollen stored at −196 °C yielded significantly higher germination (51.5 %) after 24 h, and long-term storage (90 days) was efficient for pollen at stored at −20 °C (Lora et al. 2006).

Genetic Components Involved in *J. curcas* Flowering

Evaluation of the diversity of the *J. curcas* accessions considered as candidates for large-scale production suggests that most of the materials dispersed around the world belong to a narrow germplasm pool that does not represent the natural range of distribution. The narrow germplasm pool might be the result of limited germplasm introductions and/or the use of clonal propagation as the main method for multiplication of the selections at the farm level (Ambrosi et al. 2010), or some yet to be discovered bottlenecks.

Several studies have shown low genetic diversity of *J. curcas* from India and Madagascar, but with greater variation in diversity in some materials from Mexico and Central America (Basha and Sujatha, 2007a; Basha and Sujatha, 2007b; Basha and Sujatha, 2009; Pamidimarri et al. 2009a; Pamidimarri et al. 2009b; Pamidimarri et al. 2009c; Pamidimarri et al. 2009d; Rao et al. 2009; Sun et al. 2008). In some cases, only the accessions are distinguishable, but not the individuals in each accession. According to Achten et al. (2009), this lack of diversity could be an indicator of high homozygosity in populations. However, data about phenotypic variation have not been published, especially regarding the reproductive organs. Ambrosi et al. (2010) found high genomic uniformity, low diversity (H=0.2597), and high genetic similarity (96.5 %) among commercial varieties, using RAPD and ISSR molecular markers. A set of SSR markers indicated a high degree of homozygosity (H_e=0.3491) and displayed a low fixation index (F_{ST}=0.2042).

Rao et al. (2008) reported using path analysis that the flower sex ratio exhibits a heritability of 0.9995, which has a positive direct relationship (+0.789) with the seed yield providing a genetic advance of 41.11 %. However, there was no correlation between days elapsed from initiation of flowering and maturity of fruits. There were additional significant positive genotypic and phenotypic correlations between the number of branches and number of flowers per plant and plant yield. The genetic correlation of yield with height was −0.23, and that with seed weight per plant +0.48. The authors conclude that, after its introduction to India, *J. curcas* has continued to evolve towards greater genetic diversity within and among the species, even though phenotypic variation remains small.

The results of Rao et al. (2008) do not completely agree with the results from Mohapatra and Panda (2010) who report the flower sex ratio exhibits a broad sense heritability of 0.4218 and a genetic advance of 24.45 %. Also, flower sex ratio correlates positively with number of flowers per inflorescence, number of branches per plant, days to fruiting, and days to fruit ripening, but significantly negatively to number of female flowers (−0.943) (Mohapatra and Panda, 2010). The number of inflorescences per plant showed high heritability in that experiment (88.79 %). The authors conclude that the variation in the morphological characteristics is a result of the wide geographical distribution of the species. Additionally, they do not consider that the flower sex ratio and number of flowers to be adequate selection indicators for the species.

In plants having hermaphroditic flowers, the MADS-box genes are considered to control expression of sex of the floral organs by differentially suppressing expression in specific whorls of floral organs (Ainsworth, 2000). Several research groups suggest that in the case of monoecious species, the suppression of sex in a specific organ may be a result of differential expression of the *B* and *C* genes in the MADS-box complex. However, in cucumber, the MADS-box genes did not show association with sex organ arrest (Perl-Treves et al. 1998). In the monoecious species *Liquidambar styraciflua* L. and *Rumex acetosa* L., the expression of the *C* gene has been associated with the arresting of the sexual organs in the flowers; however, in the case of *Liquidambar* the arresting could be the result of cell death, while in *Rumex* it is not clear whether arresting is the consequence or the cause of cell death (Ainsworth, 2000).

Many monoecious species progress through an early hermaphroditic stage to differentiated (unisexual) stages later in floral development, by aborting or arresting the inoperable sexual organs (Ainsworth, 2000). Cucumber exhibits this behavior especially well, with the arresting of sexual organs expressed depending on the position of the flower on the shoot (Kater et al. 2001). In *J. curcas*, the sex of the apical flowers correlates to flowering time and the sex of the rest of the flowers in the inflorescence (Li and Li, 2009). Thus, if the top flower is male, the inflorescence will not present female flowers; in contrast, if the top flower is female, there is an 80 % probability that female flowers will be present in the inflorescence. Wu et al. (2011) propose that *J. curcas* bears three types of inflorescences: female, male and intermediate, arguing that the sex of the flowers depends of the position of the flowers in the inflorescence. Thus, the flowers on the third branch of the sub-branched inflorescence rachis are exclusively male, while the top of the main inflorescence and the middle of the first and second sub-branches can bear female flowers.

Expression of sex in cucumber is controlled by the major loci *F*, *M*, and *A*. According to Staub et al. (2008), the *F* locus influences the degree of femaleness (*FF*>*Ff*>*ff*), while the *M* locus determines whether flowers are unisexual male (*M_*) or bisexual (*mm*). The *A* locus mediates the male tendency, depending on whether the plant is homozygous recessive for *aa* and *ff*. While these loci determine the sexual behavior of cucumber, the intensity and expression of these genes are influenced by the hormones ABA, ethylene, and GA, and by environmental conditions, notably temperature (Staub et al. 2008).

One way to identify the genetic mechanisms controlling sex expression in plants involves crossings between closely related monoecious and dioecious species (members of the same species but from different varieties or subspecies, as in sub-dioecious species, in which female, male and hermaphrodite plants are present). Dioecious is the condition of a species possessing distinct (separate) male and female plants. Correns (1928) crossed monoecious and dioecious species of the genus *Bryonia* (Cucurbitaceae) and determined that the male sex is the heterogametic one. This conclusion is supported by Heilbronn (1948), who obtained progeny consisting of 50 % female and 50 % male plants when he crossed *Bryonia alba* L. (monoecious and used as the female parent) and *Bryonia dioica* Jacq. (dioecious and used as the male parent).

Dehgan (1984) made several crosses among species of *Jatropha*, some between monoecious and dioecious species. In crosses between *J. curcas* (female parent) and *Jatropha cordata* (Ortega) Müll. Arg. (male parent), the progeny were exclusively male. Plants of *J. cordata* exhibit terminal solitary female flowers (which abscise usually within 24 or 48 hours) (Dehgan and Webster, 1979). From five flowers pollinated (theoretically 15 potential ovules fertilized) five seeds and five individuals were obtained. The F_1 hybrids had exclusively male flowers.

J. curcas × *Jatropha multifida* L. hybrids yielded dioecious individuals as a result of the abortion of flowers of the other sex (Dehgan and Webster, 1979). The hypothetical explanation for this pattern was that the changes probably occurred as result of an internal hormonal control. However, vestigial sex organs have not been observed in *Jatropha* (Dehgan and Webster, 1979). The hybrids resulting from *J. curcas* × *Jatropha integerrima* Jacq. and *J. curcas* × *Jatropha macrorhiza* Benth. (the three parents are all monoecious) produced F_2 progenies, but only the progeny of the first cross produced invariably bisexual flowers.

Sex expression in castor bean [*Ricinus communis* L. (Euphorbiaceae)] has been studied since the 1950s, which provides a good model from a species close related to *J. curcas*. Typically all castor bean plants are monoecious; however, male and female plants have been reported, as well as sex reversions (female to monoecious) and hermaphroditic flowers (Brigham, 1967). In addition to having a pattern of branching stamens, the complex architecture of the castor bean inflorescence, has caused it to be used as a model in theories about plant sex-morphogenetic transitions (Prenner et al. 2008). Jakob and Atsmon (1965) proposed a quantitative genetic mechanism controlling the percentage of female progeny and the time to their reversion to a monoecious state during the ontogeny of plants of *R. communis*. They also proposed a mechanism for a genetic change, which could be transmitted through the pollen. Plants of castor bean are commonly classified into two main flower sex categories: pistillate plants exhibiting flowers possessing pistils but no stamens; or staminate plants exhibiting flowers possessing stamens but no pistils. Thus, Lavanya and Gopinath (2008) determined that the trait of exclusively pistillate is dominant over the trait of pistillate with interspersed staminate flowers (i.e. male flowers in between female flowers) and that this character is controlled by up to four genes. Lavanya (2002) reported that temperature affects sex expression and sex variation in the pistillate lines of this species. Solanki and Joshi (2000), working on pistillate lines of *R. communis*, report that additive and epistatic gene effects govern the percentage of pistillate whorls, while additive and additive × dominance gene effects control the inheritance of femaleness.

Clearly, the genetic control of sex expression in monoecious plants is complex because the expression of both sexes in different flowers but in the same plant is required. In most monoecious plants, the sexes are disposed in different inflorescences and in different locations on the plant, which suggest two different developmental programs as for example in maize. However, the male and female flowers in *J. curcas* are present in the same inflorescence, just in different locations on it; hence suggesting the operation of a more complex genetic program.

Carels (2009) suggested that information from genomic sequences from *Populus* (Malphigiaceae) may be adequate for understanding of the genetic control of sex expression display in *J. curcas*, because both Euphorbiaceae and Malphigiaceae are in the order Malpighiales, which most likely share a high degree of synteny. However, Cucurbitales and

Malpighiales are in the subclass Fabids (Eurosids I), grouped in the Rosid clade (Judd, 2008). Therefore, sex expression display in *J. curcas* may share more similarities with cucumber than with *Populus*. The genome of the cucumber has been sequenced (Huang et al. 2009) and the molecular characterization of the *M* gene has been released (Li et al. 2009). With such a characterization, the authors of that paper suggest that the cucumber *M* gene is involved in a conserved-residue conversion phenomenon. If conserved-residue conversion is present in *J. curcas* it could induce the formation of hermaphroditic flowers as a result of the original enzymatically active allele having converted to a nonfunctional form (from *M* to *m*).

Sato et al. (2011) searched for MADS-box genes across the genome sequence of *J. curcas*. They used sequences of genes already identified in *Arabidopsis thaliana* L. that are involved in the control of flowering display, flowering time, and response to environmental conditions. Sato and collaborators located 28 candidate genes related to flowering including homolog to genes such as *CONSTANS (CO)*, *FLOWERING LOCUS D*, *FLOWERING LOCUS F*, *LEAFY* and *SUPRESSOR OF OVEREXPRESSION OF CONTANS 1,* and to three floral identity genes: *APETALA2*, *APETALA3*, and *PISTILLATA*. In addition, they identified five paralogs of the *SHORT VEGETATIVE PHASE (SVP)* gene which is greater than the number of *SVP* genes reported in *A. thaliana* or rice). *SVP* plays an important role in the response of *A. thaliana* to ambient temperature changes. Also, sequences homologous to the *CO* locus were identified. *CO* is involved in the regulation of flowering by photoperiod in cereals such as rice and barley. The identification and quantification of these candidate genes and paralog sequences suggest that the molecular and genetic components involved in the floral identities of *J. curcas* can be elucidated.

Environmental Factors Involved in *J. curcas* Flowering

Dehgan and Webster (1979) suggested that the inflorescence characteristics of *J. curcas*, such as sexual ratios, could be altered by photoperiod. However, no experimental evidence to date supports this hypothesis. Subsequent studies documenting various sex ratios in the flowers (Abdelgadir et al. 2009b; Ashoke et al. 2005; Luo et al. 2007; Raju and Ezradanam, 2002) raise questions about: what factors most strongly affects the flower sex ratio in *J. curcas*? How influential is the photoperiod? Is it more influential than temperature? What about the interaction between them? What is the relevance of the genetic component?

In a study using the Geographic Information Systems (GIS) and phenological data from 100 accessions of *J. curcas* from different locations in India, grown in the same experimental field, Sunil et al. (2009) reported that initiation of flowering for the species could be grouped into five categories: very early (35 %), early (29 %), medium (10 %), late (20 %), and very late (6 %). Moreover, oil content and other morphological characters, including plant height, plant spread, collar length, number of primary branches and fruit clusters per plant, varied widely. While these authors did not relate environmental factors with the pattern of flowering per accession, a relationship may exist. They also identified promising places to collect germplasm with respect to fruits per cluster and oil content using the rarefaction method implemented in DIVA-GIS.

The summer flowering of irrigated 3-year-old *J. curcas* plants, grown in the Imperial Valley of California, −16 m below sea level at 32º 48’ N and 115º26’ W having an arid low latitude desert climate, was highly affected by temperature (Fig. 3). The arid low latitude desert climate (B_{Wh}) present in the Imperial Valley of California exhibits largely unbroken sunshine for the whole year due to the stable descending air and high pressure. This climate is characterized by 74.2 mm of rainfall per annum, 25 % relative humidity, and monthly mean temperatures oscillating between 12.8º C and 32º C, and maximum temperatures in the summer of 47º C. Such extreme temperature fluctuations induced early abortion in the male flowers (Fig. 3a and b) and inhibition of opening for the female flowers during the day (Fig. 3c). Few fruits were present during the subsequent weeks (Fig. 3d), and those that were present were small, with just one or two seeds (Fig. 3e), and those seeds were empty (Fig. 3f), which suggests parthenocarpic formation of the fruits. *J. curcas* plants grown in the Imperial Valley would not depend on stimulation by pollination, since there was an absence of pollinators and a scarcity of pollen. The occurrence of viviparity (germination of seeds in the fruit) has been reported in environments with less extreme fluctuations in temperature and high relative humidity (Deore and Johnson, 2008).

Flowering is a trait clearly exemplifying environmental influences. The expression of flowering sex ratios in crops such as cucumber (monoecious, but with trimonoecious exhibition) and papaya (*Carica papaya* L., a species considered as polygamous in exhibiting more than one mode of reproduction) is regulated by the interactions of specific genetic components and environmental factors such as temperature, photoperiod, soil nutrient availability and hormonal relationships. Thus, it is possible to see flower sex reversions in cucumber (female to male) triggered by temperatures between 35 and 38 °C. In papaya, flowers can transition from hermaphroditic to carpelloid (i.e. state of a flower due to the transformation of stamens into carpel-like structures) and pentandric types (i.e. flowers in which a hermaphroditic flower transforms into a female flower, sometimes exhibiting a reduced number of stamens and an ovary with deep grooves), or exhibit stamen abortion, or

Fig. 3 Effects of high temperatures and low humidity on the flowers, fruits and seeds of *J. curcas*. **a** abortion of male flowers. **b** death of male flowers and evident chlorosis of the female flowers. **c** Inhibition of the opening of female flowers under the worst conditions of temperature and humidity; the male flowers died. **d** The limited fruit setting in the orchard as a consequence of adverse environmental conditions. **e** two-seed dry fruits; typically three seeds are formed. **f** empty seeds; the absence of an embryo suggests parthenocarpy in *J. curcas* as a result of adverse growth conditions

ovarian atrophy. These variations occur mainly at extreme temperatures, high moisture, high soil nitrogen levels, and water stress (Arkle and Nakasone 1984).

Plant sex ratios cannot be considered a conservative trait as the earlier cited data on heritability suggest. Rather sex ratio and floral sex allocation are considered sequentially variable (Brunet and Charlesworth 1995; Niesenbaum 1992), because flower sex ratio and floral sex allocation arise from several complex processes. Although these processes are genetically regulated, they are highly dependent on environmental and physiological factors, acting through transposable elements and epigenetic phenomena such as methylation and demethylation, (Martin et al. 2009).

Sex expression in monoecious plants is usually considered labile in relation to environmental conditions. Glawe and de Jong (2005) assessed flower sex ratios in clones of monoecious plants of *Urtica dioica* L. under various environmental conditions, finding that, under favorable conditions, 43 % of the clones produced exclusively staminate flowers. The authors relate the exclusive production of staminate flowers to arrested hormone production that was triggered by nutrient availability. However, data on endogenous hormone levels was not provided. Basically, the framework that they proposed is that hormone balance directs differential allocation of nutrients and energy to a specific sex, which subsequently alters the sex ratio. Hence, arresting the development of one of the sexes in preference to the other sex may be a survival strategy for some species.

Additional recent studies of the regulatory pathway of flowering in monoecious plants also claim that environmental factors such as photoperiod and temperature act on the concentration and movement of endogenous hormones that influence flowering. Perl-Treves and Rajagopalan (2006), for example, report that short days and cool nights promote femaleness in cucumber, whereas long days and warm nights promote maleness. The authors propose that photoperiod controls gibberellin concentration while temperature controls the concentrations of ethylene and auxin. Once again, no measurements of hormone concentrations in different organs of the plants were reported.

A similar framework has been proposed for oil palm (*Elaeis guinensis* Jacq., also a monoecious plant, see Adam et al., 2011). The framework is based on phenological observations of features with respect to climate. In such a framework the presence of the sex organs is a result of genetic control, but the flower sex ratios change because they are affected by environmental factors such as levels of carbon assimilates (i.e. by sink-source imbalance relations), water availability, and photosynthetic activity. The influence of these environmental factors has been proposed to operate through a change in hormone status resulting in the arrested development of specific sex organs.

Endogenous plant hormones are considered as signaling elements intermediating between the water-carbon balance and sex determination, but the processes have not been elucidated. Additionally, the idea that sex determination and the formation of sexual organs are regulated as a physiological response to both genetic and environmental factors is commonly accepted (Ainsworth et al., 1998). A combination of techniques, approaches and data coming from functional genomics, metabolomics, phenomics and phenological observations in the field is highly desirable for the confirmation or adjustment of the proposed frameworks for monoecious plants such as *J. curcas*, oil palm and cucumber.

Dehgan and Webster (1979) suggest that species of the *Jatropha* genus cannot undergo the change from monoecious to dioecious through hormonal treatments. According to Dehgan and Webster, the dioecious condition of a *Jatropha* species appears to be unreversible. Abdelgadir et al. (2009a) applied a growth regulator treatment to a set of *J. curcas* in the field, each plant being subject to treatment by one of four regulators at one of four concentrations: N^6-benzyladenine (BA) at 3.0, 6.0, 9.0 and 12.0 mM; 2,3,5-triiodobenzoic acid (TIBA) at 0.5, 1.0, 1.5 and 2.0 mM; 2,3:4,6-di-O-isopropylidene-2-keto-L-gluconic acid (dikegulac, DK) at 2.0, 4.0, 6.0 and 8.0 mM; and 1,2-dihydro-3,6- pyridazinedione (maleic hydrazide, MH) at 2.0, 3.0 and 4.0 mM; they failed to observe any changes in sex expression levels, and the changes in vegetative growth were minimal.

Genetic-Environmental Interactions Involved in *J. curcas* Flowering, and its Manipulation

Behera et al. (2010) evaluated several production practices (topological array, fertilization, pruning and watering) in Gwalpahari, Haryana, India. They concluded that irrigation is a "critical input" under their conditions. They consider the minimum rainfall for a harvestable yield to be between 500 and 600 mm per annum for dryland farming production conditions. The climate of the area in which the study was performed was a warm subtropical climate with very cold and dry winters, which in the Köppen's classification is denominated a sub-tropical steppe climate (B_{Sh}) in which the geographic region loses more water via evapotranspiration than falls as precipitation; the rainfall is typically less than 250 mm per year and in some years no precipitation occurs at all. Additionally, during the study, plants without irrigation exhibited a reduced physiological performance (the parameters reported were Chlorophyll b, total Chlorophyll, and content of carotenoids and proteins in the leaves), compared to plants provided with various irrigation regimes. The authors recommended irrigation at 30-day intervals under similar conditions.

The impact of extreme climates on *J. curcas* was evident in the Imperial Valley experiment as excessive vegetative growth with plants reaching 3 m in height during the second year and having a stem girth of 110 mm. Under these conditions, reproductive expression was almost completely repressed. Therefore, strategies for improving the expression of anthropocentric traits in *J. curcas* have been based largely on manipulation of irrigation. Application of plant growth regulators, such as ethylene, was tested but they failed to produce visible changes. Perhaps, high night temperatures stimulated vegetative growth only and did not affect the expression of flowering. New strategies could be employed based on the use of shade houses to buffer the summer and winter thermal oscillations, the use of pollinators to promote cross-pollination, and the use of intermittent mist systems to increase the relative humidity and manage the microclimate of the field. However, the use of such inputs in *J. curcas* production would increase costs, making the cropping of *J. curcas* no longer an economic option.

According to a global mapping model for the production of *J. curcas* developed by Trabucco et al. (2010) extreme environmental conditions could expand to numerous countries over the next 10 years as a result of climate change. The authors of this model did not include an analysis of the impact of new agronomic practices or data about improved genotypes of *J. curcas* because these data were not yet completely developed, validated, and available. Trabucco and co-workers developed their model based on the natural occurrence of the species; and thus, includes a measure of uncertainty. Nevertheless, the authors claim that, although agronomic and genetic improvements could encourage the production of *J. curcas* worldwide, the performance of the species at the local level will depend on the environmental conditions in which it is produced.

Up to this time, genotype-environment interactions on reproductive traits have not been assayed from a quantitative genetics perspective in multiple locations at various times. Dellaporta and Calderon-Urrea (1993) suggest that, in the genus *Mercurialis* (Euphorbiaceae)—which has some monoecious and polyploid species with hermaphroditic flowers—flower sex reversions can be induced by hormonal treatment. This phenomenon indicates that hermaphroditism and sex reversal could be indicators of a sexually bipotent primordium in *J. curcas*. In *Mercurialis annua* L., a dominant gene influences the degree of sensitivity to feminization by cytokinin, while exogenous auxin treatment promotes maleness (Dellaporta and Calderon-Urrea, 1993). For this species, susceptibility to the application of hormones promoting femaleness and maleness is considered a heritable trait (Durand, 1969).

Abdelgadir et al. (2009c) recommend the application of indoleacetic acid (or ethylene) at the bisexual stage, to manipulate floral identity and obtain pistillate plants. Abdelgadir et al. (2010) assessed individual applications of several plant growth regulators. They found that BA, TIBA, MH and DK promoted a greater formation of flowers per plant, which consequently increased the number of fruits per bunch, increased in the size and weight of fruits and seeds, and increased the seed oil content in the year after application compared to pruning based management. The authors remark that MH could promote significant increases in the yield components of *J. curcas* because of its chemical pruning action. However, more studies of the interactions between this plant growth regulator and the environment are needed.

Vijay et al. (2010) report that the application of gibberellic acid (GA_3) to *J. curcas* in concentrations from 10 to 100 ppm hastened flowering, increased the rate of flower development, and increased the number of female flowers (with a change in flower sex ratio from 1:24 to 1:13), which then increased the final fruit yield. However, at 1000 ppm, the authors observed fruit fall. The action of the GA on the flowering of *J. curcas* indicates the activation of *LFY* signaling in the floral meristem and the action of the *AP1* promoter was suggested by Vijay and collaborators. A more thorough understanding of these phenomena would contribute to the development of a model for the behavior of the flowering of *J. curcas* in various environments.

Ghosh et al. (2010) report a 1127 % increase in seed yield of *J. curcas* in the year after application of the gibberellin antagonist and thus growth inhibitor paclobutrazol [(2RS, 3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1H-1,2,4-triazol-1-yl) pentan-3-ol]. The trial was conducted in Chorvadla, Gujarat, India that had a mean rainfall 882 mm. The treatment with 1.35 g of active ingredient per meter of canopy diameter significantly increased the female flower sex ratio, producing an average increase of 9 to 13.4 female flowers per inflorescence. Data was recorded for the amount of N:P:K removed from the soil by the seeds; the values are rounded to 23:5:24 kg per hectare. The authors also report an initially high physiological performance in the plants, expressed as higher concentrations of Chlorophyll a and b in the leaves of the treated plants. Ghosh and collaborators claim that the increase of flowering and fruiting in *J. curcas* may be a result of the florigenic properties of paclobutrazol and the subsequent interference in gibberellin biosynthesis, which confers the ability to redistribute assimilates among the plant organs, directing them to reproductive growth. This paper highlights the need to thoroughly investigate the phenomena behind the differential flowering in *J. curcas* and its hormonal balance. Such results support the hypothesis that low seed production in *J. curcas* may be a result of excess vegetative growth induced by an unfavorable endogenous hormonal balance, which competes with growth and reproductive development. However, the authors acknowledge that their initial findings were ambiguous.

A recent study performed by Pan and Xu (2010) suggests that applications of BA can also induce femaleness, by increasing of the number of female and bisexual flowers. This alteration in the flower sex ratio of *J. curcas* was exhibited after an application of 160 mgL^{-1} of BA to one-year-old plants grown in the Tropical Botanical Garden of the Chinese Academy of Sciences in Mengla, Yunnan, southwest China. The trial was conducted under 1493 mm rainfall, average humidity of 85 % and mean temperature of 21.8° C at 580 m above the sea level. The female flowers constituted up to 30 % of the total flowers per tree, and the flower sex ratio changed from 1:13.4 to 1:2.4. A significant negative correlation between fruiting rate and femaleness (number of female and bisexual flowers per inflorescence) was observed for plants treated with BA. Pan and Xu claim that such behavior could be the result of two phenomena: a lack of final photosynthetic products to supply the inflorescence and the limited space available for fruit development in the inflorescence after the increase in flowering. Pan and Xu propose interesting models to explain the change in the sex flower ratio promoted by the application of exogenous BA. They claim that the feminizing effect of the BA on *J. curcas* could be a result of the role of a cytokinin in the regulation of inflorescence meristem activity and size, as had been proposed by Werner and Schmulling in 2009 and Kiba and Sakakibara in 2010. The authors conclude that more studies of the role of cytokinins in floral development and sex determination in *J. curcas* are needed.

Concluding Remarks

The mating system of *J. curcas* may be considered a facultative mixed system between geitonoamy and xenogamy, with apomixis added, and entomophilous pollination. However, the factors leading to the various mating systems are not yet known. The genetic control of sex expression in monoecious plants is complex, because it involves the expression of both sexes in different flowers on the same plant. In *J. curcas*, the male and female flowers are present in the same inflorescence, just in different locations; hence, the genetic program may be more complex than that in plants such as maize which is also monoecious; however, with the male and female flowers in a different location. *Populus* and cucumber exhibit patterns of sexual expression similar to that of maize.

Flower sex ratios in *J. curcas* can be altered by photoperiod, relative humidity, temperature, soil nutrient availability, and exogenously applied growth regulators. A thorough evaluation of the mechanism(s) of action of each of these factors and their interaction is pending. Hence, the *J. curcas* sex ratio cannot be considered a conservative trait because it results from several complex processes. These processes are genetically regulated, but highly dependent on environmental and physiological factors, and include epigenetic control over gene expression. Thus, the sex expression in monoecious *J. curcas* can be considered labile.

Future, research on *J. curcas* for the purpose of developing it into a domesticate crop can take many fruitful directions and involve promising scientific approaches. Commercial breeding for the improvement of *Jatropha curcas* depends on basic and applied research, and the manipulation of phenomena such as flowering, either genetically or environmentally, will allow producers to exploit favorable characteristics of the species.

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