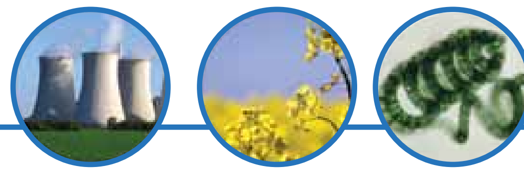
Review

Towards domestication of *Jatropha curcas*



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Jatropha curcas L. attracts a lot of interest as a biofuel crop, triggering large investments and rapid expansion of cultivation areas, and yet, it should still be considered as a (semi-)wild, undomesticated plant. To use the full potential of *Jatropha* and to support further expansion and systematic selection, breeding and domestication are a prerequisite. This review reveals and identifies gaps in knowledge that still impede domestication of *Jatropha*. Prebreeding knowledge is limited. In particular, the regeneration ecology and the degree of genetic diversity among and within natural populations in and outside the center of origin are poorly studied. There is only a limited understanding of the *Jatropha* breeding system and the effect of inbreeding and outbreeding. This review presents all currently available and relevant information on the species distribution, site requirements, regeneration ecology, genetic diversity, advances in selection, development of varieties and hybridization. It also describes possible routes to a better *Jatropha* germplasm, gives recommendations for tackling current problems and provides guidance for future research. We also discuss the participatory domestication strategy of *Jatropha* integration in agroforestry.

***Jatropha curcas* L.** (further referred to as *Jatropha*) is a rapidly emerging biofuel crop currently attracting a lot of interest and investments [1]. This stem-succulent [2] deciduous tree or shrub produces seeds rich in toxic oil (27–40% [3]). The oil can be extracted easily with techniques of different sophistication levels [4,5]. The crude *Jatropha* oil meets the fuel quality standards of rapeseed [6] and can be easily converted into **biodiesel**, meeting US and European standards [7,8]. However, although the downstream processing is well known, the species' agronomy and, as such, the potential seed production, is still shrouded in uncertainty.

Popular claims on drought tolerance, low nutrient requirement, pest and disease resistance and high yields [9] have triggered a *Jatropha* hype [4,10] with sky-high expectations on simultaneous wasteland reclamation, fuel production, poverty reduction and large returns on investments [11]. However, many of these claims are yet to be supported by scientific evidence [4,12]. Major knowledge gaps concerning basic ecological and agronomic properties (**growth conditions**, input responsiveness of biomass production, seed yield and the species' genetics), make seed yield poorly predictable [4,10]. Considering the current expansion [1], this situation might hold considerable sustainability risks (economic, social and environmental) [3]. Among other issues, the water requirement [2] and water footprint (amount of water needed per GJ biodiesel) [13,14] of *Jatropha* are still poorly understood. A better knowledge of these agronomic properties is vital for the further application of the species. *Jatropha* can still be considered a (semi-)wild, undomesticated plant showing considerable performance variability [4,10,11].

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Key terms

Jatropha curcas L.: Perennial stem succulent shrub of the spurge family, the seeds of which contain an inedible oil that can be converted into biodiesel

Biodiesel: Vegetable oil or animal fats converted to (m)ethylesters as an alternative fuel for diesel engines

Growth conditions: Conditions under which a species can naturally occur

Breeding: Changing the genetics of plants or animals for the benefit of humankind (e.g., through selection or molecular techniques)

Genetic diversity: Total number of genetic characteristics in the genetic makeup of a species

Species distribution: The spatial (uniform, random or clumped) and temporal arrangement of a species throughout its range

Regeneration ecology: Collective name of flowering, fruiting and other reproduction characteristics of a species

In order to reduce the risk of future unsustainable practices and to improve future crop performance, further selection, **breeding** and domestication of *Jatropha* is primordial. However, substantial prebreeding knowledge is important to facilitate and guide an effective and robust route towards its domestication [15]. Knowledge about the degree of **genetic diversity** among and within natural populations in and outside the center of origin is required to gain the first ideas about where to find potentially valuable genetic material. Further knowledge is needed on the reproductive biology of *Jatropha,* including its phenology, mating patterns in populations, possible pollinators and the breeding system, in order to design suitable breeding and deployment strategies. Finally, a screening of origins across the distribution area for key agronomic traits will help in choosing the basis for further work and support the initial selection efforts.

At present, no major systematic exploration and evaluation of genetic resources has been published and only little and scattered knowledge is available on the basic reproductive biology of the species. Also, limited information has been published on quantitative genetic variation, such as heritability, and genetic variance components, genotype by environment interaction, germplasm pathways and juvenile mature correlation. Such genetic variables are of key importance for conducting breeding programs [16]. The lack of knowledge will limit planting programs from using the full potential of *Jatropha.* Establishment and public sharing of prebreeding knowledge is therefore important for effective domestication of *Jatropha.*

The objective of this review is to synthesize relevant information on the ecological attributes and breeding potential required for germplasm improvement, utilization and domestication of *Jatropha*.

Species distribution & site requirements

The delineation of the original area of **species distribution** of *Jatropha* has been the subject of a long debate [17] but, currently, there is a growing agreement that the *Jatropha* center of origin is Mexico and continental Central America [17–19].

The Portuguese learned about *Jatropha's* medicinal properties in the 16th Century, and later established commercial plantations for soap and lamp oil production on the Cape Verdian Islands and Guinea Bissau [17]. Later, *Jatropha* genotypes adopted in Western Africa were spread across other Portuguese colonies in Africa (Mozambique, Angola) and into Asia (India, China and Indonesia) [17]. *Jatropha* now grows pantropically, from Brazil to the tropical islands of Fiji [201].

The climatic conditions of locations where the species is found under natural conditions within the center of origin are given in **Table 1**. *Jatropha* distribution occurs naturally under an annual precipitation ranging between 944 and 3121 mm, and a length of growing season (the number of months in which the mean precipitation is higher than half of the potential evapotranspiration) between 5 and 11 months [20].

In its natural area of distribution, the species is most abundant in tropical savanna and monsoon climates (A_m and A_w climate types according to Köppen classification [21]) and in temperate climates without a dry season and with a hot summer (C_{fa} [21]), while it is uncommon in semiarid climates (B_s [21]) and totally absent in arid climates (B_w [21]) [20]. The Cape Verdian Islands, where *Jatropha* was first successfully introduced and grown for commercial use, have a typically Sahelian climate, with a strong oceanic influence [22]. Mean annual vertical rainfall varies between 100 mm on the coastal flats to 900 mm at the highest elevations, with strong support of oceanic humidity (unrecorded by standard pluviometers) and mild annual and daily temperature changes. In its distribution of herbarium specimen locations recorded in Eastern Africa, where it was probably introduced using genotypes from Cape Verde, *Jatropha* is established in locations with annual precipitation ranging between 650 and 2500 mm, and length of growing season between 4 and 12 months. These latter results were derived by replicating the published methodology for *Jatropha* specimen locations in Eastern Africa [20].

Table 1. Mean, optimal range (25–75% percentiles) and total range (5–95% percentiles) of climate variables for the locations of *Jatropha* specimens found in the area of natural distribution of *Jatropha* (n = 241).

Statistic	T_{mean} (°C)	T_{min} (°C)	T_{max} (°C)	P_a (mm/year)	LGS (# months)	AI (/)
Mean	24.4	16.5	32.5	1689	7.3	1.04
Optimal range	23.4–26.2	14.4–19.4	31.5–34.0	1207–2001	6–9	0.73–1.19
Total range	19.3–27.2	10.5–21.2	27.4–35.7	994–3121	5–11	0.55–1.99

AI: Aridity index: the ration of mean annual precipitation to total potential evapotranspiration; LGS: Length of growing season; P_a: Annual precipitation; T_{max}: Maximum daily temperature of the warmest month; T_{mean}: Mean annual temperature; T_{min}: Minimum daily temperature of the coldest month.
Data from [20].

Regeneration ecology

Jatropha is monoecious – with male and female flowers on the same plant and in the same inflorescence [23,24]. Studies on pollination biology have been carried out outside the natural range of the species [23–25]. The size of the raceme inflorescences, with dichasial cyme pattern, can vary considerably (5–9.5 cm in length and 4.5–12.5 cm in diameter) and with this variable size, the number of flowers also varies **(Table 2)**. Note that, although the number of male and female flowers per inflorescence varies a lot among the observations [23] (male: 25–238 and female: 1–19), the male-to-female flower ratio of the two studies reporting it is similar (24.5:1 [24] and 29:1 [23]).

Male flowers are small and plate shaped [23]. The five sepals (5 mm long) and five petals (7 mm) are free [24]. The latter are connivent at the flower base, forming a short tube [23]. Ten diadelphous stamens are arranged in two tiers of five. The lower tier is free, while the upper tier is united [23]. The anthers are yellow, approximately 2 mm, dithecous and dorsifixed. Five oval-shaped glands are present at the villous flower base. The anthers dehisce 1 h after flower opening by longitudinal slits. The pollen produced are globular and their size ranges from 52 to 89 µm **(Table 2)** [23,24]. The floral base contains 0.3 µl nectar.

Female flowers show a similar shape as the male flowers [23,24]. The flowers contain three styles and bifid stigmas. The ovary has three carpels, each with a single locule producing one ovule. The floral base is villous and contains five yellow elliptical glands under the ovary [23,24]. The stigmas are receptive during 3 days after the opening of the flower. The flower base secretes nectar [23]. Although Raju & Ezradanam report that the female flowers secrete the same quantities of nectar as the male flowers [23], Bhattacharya *et al.* observed a higher nectar production in female flowers (4.54 ± 0.82 µl in 1200 h) than male flowers (1.92 ± 0.44 µl in 1200 h) [25]. The reported pollen ovule ratios are given in **Table 2**.

Research on the existence of a system to promote out-crossing and minimize self-pollination in *Jatropha* is scarce. Temporal dioecism is often seen in monoecious plants with unisexual flowers, but observations of opening periods of male and female flowers that overlap rejects this temporal dioecism hypothesis [23,24]. However, Chang-wei *et al.* described the opening sequence of the flowers [24]. They observed that male flowers start opening from the first or second day of the inflorescence life (13–19 days). Although the male flowers open evenly spread over this period, a small peak could be observed in the open-to-total male-flowers ratio during the ninth and 13th day. The pollen viability reduces considerably from the second or third day after dispersal. The opening of female flowers is more concentrated between the third and fifth day. In this period, 60% of the total female flowers open. Female flowers remain open for 3 days. Based on these observations, Chang-wei *et al.* conclude that this mass opening mechanism of female flowers can promote outcrossing and minimize self-pollination [24]. Based on their estimation of the outcrossing index (OCI = 4) [26], Chang-wei *et al.* categorize *Jatropha* as an out-crosser that is self-compatible and needs pollinators [24].

Table 2. Flower and pollen characteristics of *Jatropha curcas*.

Male per inflorescence	Female per inflorescence	Male:female	Total P per male	P:O	Ref.
25–93	1–5	29:1	655	6332:1	[23]
17–105	2–19		1617 ± 100	539:1	[25]
49–238	0–17	24.5:1	1597–5763	13,015–46,968:1	[24]

O: Ovule; P: Pollen.

The adhesiveness of the pollen, the smoothness of the stigma of 1.62 mm in diameter and a pollen flow by wind of 2.8 grains cm^{-2} make wind pollination almost impossible [24]. The bright yellow anther color, male flowers opening evenly spread over the inflorescence life span, the fragrance and nectar availability of both male and female flowers and the large pollen (52–89 µm), with many verrucae on their exine with adhesion, suggest insect pollination to be the major pollination method [24]. Observed insect visitors mainly belong to the order of the Hymenoptera **(Table 3)**. Raju and Ezradanam observed that of the total foraging visits made by insects on male flowers, bees contributed 34%, ants 61% and flies 5% [23]. On female flowers, bees made up 28%, ants 70% and flies 2% of the total. Bhattacharya *et al.* observed the major abundance in the *Apis* genus (honey bee; 71%) [25].

Genetic resources, diversity & characterization of breeding systems in *Jatropha curcas*

▪ Breeding, inbreeding & the potential of releasing vigor & productivity through smart outcrossing

Inbreeding depression in tree species is the process by which self- or related matings lead to homozygosity and the accumulation of deleterious mutations [27–29]. Inbreeding depression reduces individual fitness, survival and growth variables [30], and raises the possibilities of population and/or species extinction [31–33]. The negative effects of inbreeding in trees are well documented and include embryo abortion, limited fruit set, reduced overall seed yield and lower germination rate [27].

Furthermore, selfed or inbred progeny can suffer from lower seedling vigor and poor growth form, and end up being less productive when they reach maturity [34–38]. Inbreeding depression is worsened by the large variations in fecundity often observed in tree species [39,40]. This phenomenon, in which a small number of trees contribute disproportionately to the seed crop, can result in the effective population size of a tree (*Ne*) – the size of an 'idealized' population that would

Table 3. List of insects observed to visit *Jatropha* flowers and corresponding forage type they collect .

Order	Family	Genus	Species	Forage type	Ref.
Coleoptera					[24,25]
Diptera	Calliphoridae	*Chrysomya*	*megacephala*	Nectar	[23,24]
Hemiptera					[24]
Hymenoptera	Apidae	*Apis*	*florae, indica, dorsata, mellifera, cerana*	Nectar and pollen	[23–25]
	Anthophoridae	*Ceratina*	*simillima*	Nectar and pollen	[23]
	Eumenidae	*Eumenes*	*conica*	Nectar	[25]
	Formicidae	*Camponotus*	*compressus* spp.	Nectar	[23]
		Crematogaster	spp.	Nectar	[23]
		Solenopsis	*geminata*	Nectar	[23]
		Pheidole	*spathifer*	Nectar	[23]
	Halictidae				[23]
	Vespidae	*Vespa*	spp.	Nectar	[25]
Lepidoptera	Pieridae	*Catopsilia*	*pomona*	Nectar	[24]
Thysanoptera	Thripidae	*Scirothrips*	*dorsalis*	Nectar and pollen	[23]
		Trips	*hawaiiensis*	Nectar and pollen	[23]

Adapted from [23].

Jatropha is not only able to reproduce via selfing, but also through apomixis (without sexual reproduction) [24]. However, the issue with contrasting traits apparently present in the breeding system seems not to be fully clarified (Table 4). Preliminary studies indicate very low variation in microsatellite simple sequence repeat (SSR) markers within populations of *Jatropha* even in its natural distribution (Mexico) [47]. Pamidimarri *et al.* applied SSR, amplified fragment-length polymorphism (AFLP) and random amplification of polymorphic DNA markers to discriminate between two Mexican accessions of *Jatropha* (one toxic and one non-toxic) [48]. Although they could discriminate between the accessions, they found no variation between individuals within each accession.

have the same genetic properties as that observed for a real population – being much lower than the census size, and lower than that required to maintain heterozygosity and productivity [41,42]. *Ne* is also lowered if the reproductive connectivity between trees in a landscape is weak. Connectivity depends on the density and evenness of distribution of sexually mature individuals in the landscape and, if a species relies on animal pollinators and/or seed dispersers, on the presence of these agents to facilitate gene flow [43].

As explained above, *Jatropha* can set seed after both insect and self-pollination. However, self-pollinated fruits are lighter in general [44] and aborted before maturation in 25% of cases [23]. This could be due to early acting inbreeding depression [45,46] and, thus, may reflect a high natural outcrossing rate. Chang-wei *et al.* suggested that

This could be an indication of a population structure with a high level of homozygosity as well.

It is important to confirm or deconfirm the hypothesis of nonpanmictic breeding, because understanding the breeding pattern is central for design of domestication strategies. Breeding, large-scale mass propagation and distribution across landscapes will obviously be much easier if the species is reproducing by natural selfing without inbreeding depression or, especially, if it reproduces by apomixis [49].

Genetic diversity between populations

The genome size of *Jatropha* is fairly small (2C DNA content of 0.850 ± 0.006 pg or C DNA content of 0.416×10^9 base pairs) compared with other members of Euphorbiaceae [50–52]. The level of genetic diversity and

Table 4. Overview of life history traits with ecological and genetic importance.

	Trait and alternate state		Remarks
Breeding system	**Sexual** **Outcrossing** **Self-incompatibility?** **Monoecy**/dioecy	**Apomixis?** **Self-fertilization** **Self-compatibility** Hermaphroditism	Apomixis unusual Pollination by insects
Age at maturity	**Precocity**	Delayed	First fruits at the age of (2–)4–5 years
Seed crop variation	Masting	**Nonmasting?**	
Seeds:			
▪ Size	**Large**	Small	Seeds ellipsoid, 1–2 cm long
▪ Dispersal	Far	**Near?**	
▪ Dormancy	**Dormant**	Nondormant	Orthodox storage
Senescence	**Senescent**	Immortal	Lifespan of 30–50 years

Traits of *Jatropha curcas* discussed in the literature are printed bold.
Data from [23,24,44,50,51].

genetic differentiation in *Jatropha* populations deserves special attention due to its introduction history as an exotic species in many countries. In such a situation, plant populations may result in a complex genetic history, including several potential genetic bottlenecks [53,54]. Given the successive introductions of *Jatropha* and its ability of clonal mass propagation within a short time, it is possible that all African and/or Asian populations result from a narrow germplasm origin [51,55]. Genetic bottlenecks resulting from such founder effects are also known in other important **(agroforestry)** crops, most notably coffee and banana [56–58]. 'One-off' introductions are of particular concern if they are already of narrow genetic base, and/or represent low quality or poorly adapted material. Many tropical trees in farm landscapes also demonstrate both extremely low densities and highly aggregated distributions, which – even if long-distance pollen transfer is possible – will reduce effective population sizes and promote inbreeding [27]. Data on other tree species that propagate vegetatively show comparable concerns of genetic erosion [59]. Species that are reproduced vegetatively are vulnerable for clone losses, unless new clones are introduced or old clones redistributed. Generally, a certain number of individual clones respond more successfully to propagation and simple mathematical simulation models show that, after some generations, only a few clones may dominate an area [57].

Recent studies based on genetic markers uncovered surprisingly low levels of genetic diversity in *Jatropha* landraces from China [47] and only modest levels of diversity in India [60,61], indicating that the gene pool applied at a large scale may rest on a fairly fragile genetic foundation. Tatikonda *et al.* studied the diversity of 48 accessions from India based on AFLP markers and found 680 polymorphic fragments, which provided discriminative power for the classification of germplasm accessions into five major clusters [62]. There are limited published data characterizing the genetic variation in the African gene pool. Basha *et al.* included accessions from Egypt and Uganda, which in general clustered closer to the Asian landraces compared with the Mexican accessions [63], although the emerging pattern was not completely clear. Regarding the level of genetic variation within African populations, preliminary results based on SSR markers and AFLP markers indicate surprisingly low levels of genetic diversity in landraces from Mali, Kenya and Tanzania [Nielsen LR *et al.*, Unpublished Data]. Correlations of growth and oil production with DNA polymorphism have not yet been investigated.

Species with naturally high levels of inbreeding ('selfers') are expected to show less inbreeding depression [64] but, at present, very little is known about *Jatropha*'s breeding system (see flower morphology above). Both the small population sizes during introduction history and the losses of introduced genotypes due to imbalanced clonal propagation by farmers may have led to purging of recessive, deleterious alleles. This could have counteracted inbreeding depression [65]. Owing to the lack of knowledge, it is indeed possible that the *Jatropha* landraces have reduced growth, due to imbedded inbreeding depression.

Given the low genomic diversity in *Jatropha* landraces, we believe that 'smart' outcrossing between superior Asian individuals with new introductions from Americas should be performed. Such crosses should release any inbreeding depression and thereby increase vigor and fruit production if genetic diversity of American landraces is effectively larger. The introduction of genetic variability can be performed by intraspecific and/or interspecific crossing. Actually, interspecific crossing experiments have successfully been carried out between *Jatropha curcas* L. and *Jatropha gossypifolia* L., *Jatropha glandulifera* Roxb., *Jatropha integerrima* Jacq., *Jatropha multifida* L., *Jatropha villosa* (Forssk.) Müll. Arg. and *Jatropha maheshwarii* Subram. & M.P.Nayar [66]. F_1, F_2 and F_3 hybrids, as well as various back-crossings, are available and should be evaluated with respect to seed production, oil yield and performance when grown under different climatic conditions [67]. The results from such studies will provide important insight in the next few years. Random amplification of polymorphic DNA markers and AFLP markers are available for interspecific hybrids identification [68].

> **Key term**
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> **Agroforestry:** Collective name for land use systems and technologies, where woody perennials are deliberately used on the same land unit as agricultural crops and/or animals, either in some form of spatial arrangement or temporal sequence

Experience with testing of seed sources & development of varieties

Until now, little information has been published on the production variability between provenances of *Jatropha*. In a study with 13 provenances and landraces tested in Senegal (two sites) and Cape Verde (two sites), significant differences of vegetative growth were found at all sites. At one of the test sites at Cape Verde, provenances were significantly different concerning the number and weight of capsules and the number and weight of seeds per shrub 25.3 months after planting [17]. Genotype by environment interactions between sites were significant in Senegal, but not in Cape Verde [17]. Ginwal *et al.* compared plants from ten Indian landraces after 6–24 months, and found large significant variations, attributing more than 80% of the total phenotypic variance to **seed sources** [69]. This is a relatively high level of genetic variability compared with what is usually found in tree species of tropical dry zones [70,71], and is especially surprising given the limited level of variation observable at the DNA level, as discussed previously.

Key term

Seed sources: Provenance of planting material

▪ Quantitative variation within provenances & landraces

Studies of the quantitative genetic variation within populations are sparse in *Jatropha*. Phenotypic studies are several, but they are often made for seed properties of genotypes standing at different sites, making it impossible to separate the effect of the genotype from the effect of the site [69,72]. Oil content assessments have shown a phenotypic range from 28 to 39% and 100 seed weight from 49.2 to 64.9 g in accessions from Indian landraces [72]. Similar results were found in another study with Indian landraces, where the oil content ranged from 29.9 to 37.1% and the 100 seed weight from 57 to 79 g in candidate plus trees (plants yielding more than 2 kg of dry seed per plant and with ages above 5 years) [18]. However, in both cases, these estimates were influenced by the site of the candidate trees. In an experiment with cuttings from 29 candidate trees evaluated after 34 months, the broad-sense heritability was high (ranging between 0.63 and 0.88) for height, number of branches, number of flowers, ratio between female and male flowers, days from initiation of flowering to fruiting, days from fruiting to maturity and seed yield per plant [18]. The genetic correlation of plant height with seed yield per plant and female-to-male flower ratio was 0.36 and -0.23, respectively, and the genetic correlation between the female-to-male flower ratio and seed yield per plant was 0.48. The number of branches was moderately correlated with seed yield per plant (genetic correlation of 0.61). The genetic correlation between number of flowers and seed yield was 0.29 and the yield per plant was moderately correlated (0.32) with days from fruiting to maturity [18]. The low genetic correlation of seed yield with the height and number of flowers suggests that the possibility of increasing seed yield through selection for these two traits is poor. Slightly better opportunities to increase seed yield are present in the case of (indirect) selections aiming at an increase in female-to-male flower ratio or number of branches.

High broad-sense heritability and a small phenotypic variation was found for plant height and root collar diameter in ten accessions [73].

▪ Genotype by environment interactions

Jatropha is cultivated under variable conditions, and one aspect of domestication is the degree to which different genotypes perform best under different growth conditions [16]. Another aspect of domestication is the performance of each provenance under different conditions. In general, a wide genetic base is essential to prevent inbreeding depression and allow for adaptation to changing environmental conditions (e.g., climate change) and to altering markets for tree species' products [27]. However, published information on this aspect of *Jatropha* is very scarce. To our knowledge, there are no studies on genetic material over a range of environments published for *Jatropha*, other than the Senegal and Cape Verde tests reported by Heller [17]. This lack stresses the importance of establishing genetic tests over a range of environments, in order to reveal possible genotype by environment interactions (provenance trials), and to determine suitable seed collection zones for superior germplasms. Actually, genotype by environment interaction in *Jatropha* is expected from investigations on other crop species of Euphorbiaceae (e.g., *Ricinus communis* L. [74,75]).

▪ Toxic & nontoxic *Jatropha*: a potential key trait in breeding programs

An important aspect of domestication of *Jatropha* is the toxicity of the plant [48]. Consumption of *Jatropha* seeds may result in various symptoms, including vomiting and diarrhea, and has proven lethal in animal experiments [76–78]. The most problematic toxic components in *Jatropha* are probably a number of phorbol esters that, in general, are found present in high concentrations in the seeds [79–81]. Phorbol esters are compounds known to cause severe biological effects, including inflammation and tumor promotion [82,83]. Removal of the phorbol esters during processing is possible [84], but this is not an easily deployed process and the presence of possibly toxic phorbol ester degradation products after treatment cannot be ruled out [81].

From the user's perspective, the toxic phorbol esters provide a potential health risk for workers and limit the use of the protein-rich press cake that otherwise would be suitable for animal diets [77,83]. Still, phorbol esters may protect the plants against pests, and will, therefore, be important when testing if phorbol ester-free *Jatropha* plants are more susceptible to damage from pests. To our knowledge, no such experiments on the insect-resistance of nontoxic versus toxic plants exist, and it is, therefore, advisable to include such studies in any breeding program that aims at removing the toxic phorbol esters from the phenotype. The fate of degradation of phorbol esters in soils is also an important aspect, because residuals from *Jatropha* oil productions (e.g., the press cake) are often applied as fertilizers [4]. Although it is claimed that the phorbol esters of the press cake decompose completely within 6 days after application to the soil [85], it is still uncertain whether crops fertilized by the *Jatropha* press cake (e.g., horticulture and cereals) can take up phorbol esters during that period [4].

For these reasons (e.g., human health, soil and seed cake use), breeding for nontoxic *Jatropha* provides interesting prospects. In this context, it is highly interesting that plants from some provenances in Mexico contain very low or nondetectable levels of phorbol esters [63,79,86–89]. The presence of naturally occurring plants with low levels of phorbol esters is very interesting in a domestication context, because it makes it likely that plant material without phorbol esters can easily be developed without the use of advanced molecular breeding or transgenic modification. However, introducing nontoxic material may raise new complications, as nontoxic and toxic *Jatropha* are morphologically alike. Additionally, close proximity of toxic and nontoxic *Jatropha* can trigger unexpected traits through cross-pollination.

Jatropha seeds also contain a trypsin inhibitor, lectins and phytate that are antinutritional factors in relation to a potential use of the press cake for animal feed [79]. The trypsin inhibitor and lectins can be removed by heat treatment and phytate is neutralized by the addition of microbial phytase [88].

Route to better germplasm

The few published results from field testing with *Jatropha* suggest quantitative genetic control of a number of traits of importance for the cultivation of the species [18,73]. Experiences from a number of dry-zone woody species have, in general, revealed very large genetic differentiation, in terms of production and suitability for growth under different climatic conditions [70]. The *a priori* expectation is, therefore, that development of improved planting material, through testing and deployment of genetically improved sources of reproductive material, will be an effective tool for enhanced production.

Fortunately, *Jatropha* is suitable for quick and efficient domestication compared with other woody species. This is due to a number of important features regarding production of oil, its propagation, establishment and adaptation of the plants:

- Short generation turnover. Recurrent selection can be performed in short intervals;
- Easy to propagate clonally;
- Native gene pools still exist;
- Techniques and experience with controlled crosses are available;
- Precocity (short juvenile phase), indicating that productivity can be assessed early, once the trees start to fruit;

Publically available information suggests that a number of different commercial and public entities are involved in the development of improved germplasm. Carels lists 22 organizations from eight countries as major international organizations involved in the genetic improvement of *Jatropha* [90]. Carels notes that ten of these are directly involved in breeding [90]. This list is by no means exhaustive and an extensive web search reveals thousands of web pages that refer to companies and organizations involved in improvement of *Jatropha* cultivars, some even for subtropical areas [202]. Still, surprisingly limited peer-reviewed documentation of superiority of specific planting material based on progeny/clonal testing is available at present.

Both decentralized, low-input breeding approaches based on farmland seed sources as more centralized germplasm procurement systems can be considered [91]. We think that farmers' involvement in testing, procurement and deployment of improved planting stock will be important, in order to ensure large-scale access to improved planting material. Still, given the limitations in genetic knowledge on *Jatropha* as reviewed earlier, a number of steps seem to be required on the route to better germplasm domestication programs. Below, we list a set of relevant steps that will, in our opinion, be of key relevance for low-input local breeding, as well as for more intensive breeding initiatives:

- Exploration of the genetic resources of global landraces compared with the Central American gene pool;
- Analysis of the breeding system of *Jatropha* by use of molecular markers;
- Determination of the effect of inbreeding and outbreeding;
- Exploration of the genetic mechanism behind the expression of toxicity by quantitative trait locus mapping and to evaluate the genetics of toxicity and oil production (i.e., type and degree of inheritance; dominance/codominance of toxicity, epigenetics);
- Estimation of the potential to improve biomass, especially oil production, traits of importance for mechanized harvesting, disease resistance and drought tolerance of toxic and nontoxic *Jatropha* when grown under different climatic conditions;
- Development of breeding and seed-transfer guidelines based on climate and soil variables, taking different farming systems and farmer preferences into account;
- Association studies based on cosegregation between genotypes and molecular markers with high resolution (e.g., SSR, ALFP and single nucleotide polymorphism markers) and exploring their use for effective marker-aided selection, either for direct deployment of identified and selected clones/seed or for inclusion in decentralized multiple breeding populations;
- Application in farmers' fields and governmental or private intense plantations.

Conventional breeding

The most important traits for the selection of candidate plus phenotypes of *Jatropha* are seed yield, seed size and oil yields [92]. In the case of mechanical harvesting, dwarfing of stocks, branching suppression and uniform ripening will also become important [93]. By setting up a seed-based breeding approach – based on breeding of offspring from provenances and open-pollinated families – several other breeding objectives could be achieved. Apart from obvious yield criteria, it is important that such a breeding approach develops planting material adapted to local environmental conditions.

Clonal propagation is highly efficient to obtain high genetic gains [94,95], since all genetic effects (additive as well as nonadditive effects) are transferred by the propagation and since selections based on clonal tests are much more precise, due to the fact that all the genetic background of a genotype is tested. *J. curcas* is easily cloned from cuttings. Pretreatment of spring branch cuttings with auxins (IAA, IBA and NAA) and thiamine stimulates rooting and sprouting [96,97]. However, rooted cuttings do not develop a taproot (in contrast to seedlings and are probably more prone to drought and wind [98]. This might limit the use of cuttings to areas with irrigation. In this context, the indication of apomixis in *Jatropha* [24] is encouraging, as it may enable breeders to grow genetically identical clones as in cuttings, but with taproots.

High yielding varieties developed in a clone-based breeding approach can be deployed as clones directly, or subsequently as components in clonal seed orchards (in cases where deployment of seedlings are preferred). This step could also include the propagation of high-producing varieties that are genetically transformed to remove toxicity, for example [93].

▪ Molecular breeding

As toxicity in terms of phorbol esters seems to be expressed qualitatively [99], it may be regulated by only one or a few genes. The inheritance of toxicity is not settled, but Sujathha *et al.* suggest that the phenotype of the mother tree is passed on to the seed (i.e., nontoxic mothers give nontoxic seed and toxic mothers give toxic seeds, independent of the phenotype of the father) [99]. Maternal inheritance (of chloroplast-specific markers) was also observed in natural and artificial intraspecific hybrids [66]. This pattern of inheritance could be explained in different ways, including hypotheses of apomixes or involvement of suppressor genes. Potentially, the nontoxic phenotype may be driven by a single suppressor gene that inhibits the production of all phorbol esters when present. Established F_1 hybrids between toxic and nontoxic *Jatropha* and first-generation backcrossing could be used to detect the genetic mechanism behind toxicity. By localizing the locus (or loci) responsible for (non)toxicity in the respective parent with molecular markers, it will be possible to use the markers for future use in breeding. Additionally, established clonal field trials can serve as material for association studies based on cosegregation between genotypes (e.g., clones with high oil content and Indian Andhra Pradesh accessions [100]) and molecular markers as, for instance, microsatellites (SSRs), AFLPs and/or inter-SSR markers. Still, more segregation studies are needed to resolve the mode of heritance of toxicity and its molecular background, as such understanding will guide the design of multiple breeding programs.

The application of genetic markers (e.g., polymorphic microsatellites [Table 5]) also makes it possible to carry out earlier selections and, thus, reduce the time between the recurrent selections and increase the genetic gains per year. Finally, the use of the markers will also help increasing breeding efficiency. The ability to reveal genetic markers associated with certain traits depends on the size of the material, sufficient polymorphic markers and precise estimates of genetic values.

Transgenic approaches may also prove important in the future [19,93]. *Jatropha* can be transformed based on *Agrobacterium tumefaciens* infection [101,102]. The approach can target removal of toxicity and antinutrient components, but work has also been carried out on the biosynthesis of fatty oils [103]. If the improved value of byproducts as livestock feed is a primary target for breeding, reduction of antinutrient factors can potentially be an interesting goal for molecular breeding, as suggested in other crops [104].

Future perspective

The current public and private interest in *Jatropha* has triggered large-scale investments and expansion of its plantations [1]. As such, genetic improvement, selection and domestication initiatives currently focus on improving *Jatropha* for its performance in large-scale monoculture plantations. However, monoculture expansion holds risks of unsustainable practice that will not be solved by domestication (e.g., land use conflicts, land right conflicts and loss of ecosystem services) [105]. Furthermore, there are specific problems with *Jatropha* monocultures, ranging from unknown best practices, to pest and disease management and to unsure economic viability. Several of these general and specific problems could be overcome by following a pathway of community-based small-scale *Jatropha* initiatives (e.g., agroforestry systems) in specific areas [106]. As such, we believe that integrating *Jatropha* into existing smallholder agroforestry systems, such as hedge and boundary planting, can form a robust and sustainable base for *Jatropha* domestication and expansion [105], and can

Table 5. 24 microsatellite primer pairs in nontoxic and toxic varieties of *Jatropha* with indication of polymorphism.

SSR primer and NCBI GenBank ID	Primer sequence (5´–3´)	T_a (°C)	Repeat motif	Expected allele size (bp)		Polymorphic	
				Nontoxic	Toxic/not specified	Nontoxic	Toxic/not specified
jcds10 (EU586340)	F:CATCAAATGCTAATGAAAGTACA; R:CACACCTAGCAAACTACTTGCA	46.5	$(TG)_6CACGCA(TG)_4$	108/122	108/122		+
jcds24 (EU586341)	F:GGATATGAAGTTTCATGGGACAAG; R:TTCATTGAATGGATGGTTGTAAGG	51.0	$(CA)_5(TA)_8(CA)_4$… $(TA)_3GA(TA)_4$	204/210	204/216	X	X
jcds41 (EU586342)	F: AACACACCATGGGCCACAGGT; R:TGCATGTGTGCGGGTTTGATTAC	56.5	$(CA)_6(TA)_2$	102/114	102/114		+
jcds58 (EU586343)	F:TCCATGAAGTTTGCTGGCAAT; R:AGGTCATCTGGTAAAGCCATACC	54.0	$(GT)_4(GA)_5$	104/112	104/112		+
jcds66 (EU586344)	F:CCTACGAGTGATTGGATAGTTTCTCA; R:TCTTCCATCAAGAGTCGTTGGGCA	54.0	$(CT)_2(GT)_3ATTGCA(AT)_4$	216/228	216/228		+
jcps1 (EU586345)	F:GAGGATATTACAGCATGAATGTG; R:AATCAATCAATCTTTGGCAAA	47.5	$(TG)_4$…$(GT)_3$…$(GT)_4$	132/162	132/162		+
jcps6 (EU586346)	F:CCAGAAGTAGAATTATAAATTAAA; R:AGCGGCTCTGACATTATGTAC	44.0	$(AT)_3G(TA)_3$…$(CT)_3$… $(GT)_5CT(GT)_3$	288/305	288/380	X	X
jcps9 (EU586347)	F:GTACTTAGATCTCTTGTAACTAACAG; R:TATCTCTTGTTCAGAAATGGAT	48.0	$(GT)_3GC(TG)_2A(GT)_3$	140/132	140/132		+
jcps20 (EU586348)	F:ACAGCAAGTGCACAACAATCTCA; R:TACTGCAGATGGATGGCATGA	55.0	$(TG)_{12}(GA)_{22}$	271/260	260/278	X	X
jcps21 (EU586349)	F:CCTGCTGACAGGCCATGATT; R:TTTCACTGCAGAGGTAGCTTGTATA	54.8	$(CA)_2$…$(CA)_4$	189/200	189/208	X	+
jcms21 (EU586350)	F:TAACCTCTTCCTGACA; R:ATAGGAAATAAGAGTTCAAA	43.0	$(CA)_7$	81/89	75	X	+
jcms30 (EU586351)	F:GGGAAAGAGGCTCTTTGC; R:ATGAGTTCACATAAAATCATGCA	48.5	$(GT)_5T(TG)_2$	135/144	144/148	X	X
JcSSR-18 (EU099518)	F:GGCGACAGGAAGAGCATG; R:GCAATCTTGGACAGGAAACG	62	$(TA)_3(GT)_{18}$		394		+
JcSSR-19 (EU099519)	F:CTTGAAAGTTTTTGTAATTTC; R:CGCCAATCATAGATC	50	$(AC)_{21}$		214		+
JcSSR-20 (EU099520)	F:GGCTGAACTTGCGCC; R:GCCCTGATTTCTGGTC	60	$(AC)_{10}$		260		+
JcSSR-21 (EU099521)	F:CTGAAATGGAGAAATTGG; R:ACATATCGAAGATAGGG	50	$(C)_7(A)_5(CA)_9$		249		+
JcSSR-22 (EU099522)	F:GAATCTCAACAGTGCCC; R:GAAGGATGGGAAGTGGG	52	$(TC)_{16}$		152		+
JcSSR-24 (EU099524)	F:CACACACAACCAAACTGG; R: GGTTCTCTGAGATCCTC	56	$(C)_6G(C)_6(AC)_5$		287		
JcSSR-26 (EU099526)	F:CATACAAAGCCTTGTCC; R:AACAGCATAATACGACTC	55	$(CA)_{18}$		211		+

T_a: Annealing temperature; bp: Basepairs; NCBI: National Center for Biotechnology Information SSR: Simple sequence repeat; X: Polymorphism shown on gel; +: Number of alleles reported > 1.
Data from [48,63,102,203].

Table 5. 24 microsatellite primer pairs in nontoxic and toxic varieties of *Jatropha* with indication of polymorphism (cont.).

SSR primer and NCBI GenBank ID	Primer sequence (5´–3´)	T_a (°C)	Repeat motif	Expected allele size (bp)		Polymorphic	
				Nontoxic	Toxic/not specified	Nontoxic	Toxic/not specified
JcSSR-28 (EU099528)	F:GCATTTAGCAGAACCCCA; R:CTAGCTAGTGTTATGTCTC	54	$(CA)_{17}$		179		
JcSSR-29 (EU099529)	F:GCCATCCAATTATGGG; R:ACAAGTAAGAAGTGAAG	50	$(CTT)_3CT(CTT)_2TG(T)_5$		156		
JcSSR-31 (EU099531)	F:CTGGTGCTAAAACTATGG; R:ACTGGTCATTCAGCTCC	52	$(GT)_5(G)_5C(G)_6$		290		
JcSSR-32 (EU099532)	F:TTAGTAGAGAACAAAAG; R:CGTTACTCTCTACCG	42	$C(A)_5G(A)_{15}$		298		
JcSSR-34 (EU099534)	F:AGAAGAAAGAGGCGAC; R:TCTTGTTGTTCATGAGG	44	$(GAA)_7$		147		

T_a: Annealing temperature; bp: Basepairs; NCBI: National Center for Biotechnology Information SSR: Simple sequence repeat; X: Polymorphism shown on gel; +: Number of alleles reported > 1.
Data from [48,63,102,203].

avoid the risks associated with monocultures. On smallholder farms, the niche for growing *Jatropha* will have to be prioritized based on need and compatibility with the existing farming system. Therefore, tree domestication should also be aimed at farmers' needs and agroforestry.

▪ Lessons learned from tree domestication in agroforestry

One of the key requirements to the widespread adoption of new crops is the availability of high-quality planting material. In order to achieve optimal and sustainable farm productivity, farmers require quality germplasm, making sure that a range of species and selected cultivars or provenances are available. This is still a major setback in *Jatropha* cultivation. In order to achieve high-quality *Jatropha* planting material, farmers and researchers need to domesticate trees together. Domesticating agroforestry trees involves an accelerated and human-induced evolution to bring species into wider cultivation through a farmer-driven and market-led process [107]. This is a science-based and iterative procedure, involving the identification, production, management and adoption of high-quality germplasm. High-quality germplasm in agroforestry includes dimensions of productivity, fitness of purpose, viability and diversity. Domestication can occur at any point along the continuum from the wild to the genetically transformed state [107] [Internal report of the strategy meeting of ICRAF's Tree Domestication Programme in Cameroon, 2000, Unpublished Data].

Most tropical tree species have not been domesticated intensively, with the exception of a number of fruit tree species (cacao and mango), some 'beverage' tree species (coffee and tea) and some timber tree species (*Eucalyptus* spp.). Most tree species, for fruit, timber, fodder and medicine, have experienced little domestication. Since domestication of trees is not similar to agricultural crops, experiences with previous tree domestication efforts are useful to increase the efficiency of the current efforts put in *Jatropha*.

Owing to their long life expectancy, the long-term viability of the on-farm tree stands depends upon the availability of a wide genetic base providing the capacity to adapt to environmental fluctuations or changing farmer requirements, such as a change in species use, planting niche or pest outbreak. The wide genetic base will reduce the risk of potential inbreeding depression. Therefore, intraspecific genetic resource management plays an important role in determining the ecological stability of farming systems based on agroforestry, including *Jatropha* production.

Until recently, *Jatropha* was mainly grown for fencing and local soap production, but awareness of *Jatropha* growing as a cash crop for biofuel is now widely known, as farmers look for alternatives to generate income. However, farmers are often unable to access (quality) germplasm [59]. Owing to this limited choice, farmers tend to plant what is available, which is often of inferior stock.

Besides focusing domestication strategies on increasing oil yield, future research should aim at producing compatible phenotypes for use as hedgerows or boundary planting. Research is needed to understand traits preferred by farmers. Efforts to overcome the current narrow founder populations and potential inbreeding problems should be part of concerted domestication programs. Such participatory domestication strategies have been demonstrated for indigenous fruit trees in Africa [108].

Farmer dynamics & landrace development

Farmer domestication and seed collection often causes a major reduction in genetic diversity [59,109–114]:

- Farmers and nursery managers often collect germplasm from a relatively small number of mother trees;
- Seeds from solitary trees or small stands are not exempt from collection;
- If introduced into a region, most germplasm for use in subsequent planting rounds is collected from the farmer's own or neighbors' farms, increasing the risk of inbreeding in future generations.

Long-distance pollination could increase genetic diversity levels. However, similar to other insect-pollinated plant species, it is more likely that *Jatropha* trees are pollinated by their neighbors than by more distant trees. Therefore, the potential of narrowing the genetic variation through seed-collecting practices cannot be dismissed.

Two main pathways are generally followed within domestication strategy in agroforestry [115,116]:

- Improvement through on-farm domestication by smallholder farmers who bring the trees into cultivation;
- Major genetic improvement through science in research stations. In recent years, scientific approaches are being integrated with on-farm domestication through participatory approaches. The advantages of participatory domestication are that it builds on tradition and culture, local experience, indigenous technical knowledge, and promotes rapid adoption by users.

The domestication of *Jatropha* in complex agroforestry systems, using appropriate strategies, offers an opportunity to return to more sustainable polycultural systems. Leakey and Akinnifesi developed three interacting and multifaceted strategies for developing clonal fruit trees in southern Africa [115]. These strategies are the foundation of sustainable domestication strategy and are based on the establishment of types of germplasm:

- One for gene resource conservation;
- One for breeding and selection for the achievement of genetic improvement;
- One for mass production of trees for commercial purposes.

The practice of this strategy is cyclical and continuous. The strategy of multiple population breeding to sustain genetic gain and maintenance of allelic diversity [15] could be pursued in several environments [117] combined with *in situ* and *ex situ* conservation populations to conserve rare alleles. Such an integrated strategy offers a new way of creating new and greatly improved crop plants (cultivars). It also offers potential for increasing benefits and incomes, and minimizing risks arising from their capacity to capture and utilize genetic variation. We believe that *Jatropha* is amenable to such participatory domestication strategies.

Implementation of small-scale domestication

Farmers do not necessarily opt for the harvest optimization, but rather harvest security. Therefore, farmers' access to good performing and well-adapted *Jatropha* accessions with a wide genetic base seems the most logical domestication strategy for small-scale farmer systems. A wide genetic base increases the sustainability of production. Other requirements for implementation of this domestications strategy are [55,108,115,116,118,119]:

- Researchers and farmers should disseminate their agronomic findings on land suitability, agronomy and integrated pest management, for example;
- Farmers will need to team up with other production chain partners to have a guaranteed offset of their production. Without market access, farmers should not embark on joint domestication programs on *Jatropha*;
- The next step will be to establish domestication and breeding programs with farmers, researchers, extension workers and, preferably, private enterprises aiming at small-scale farming and participatory on-farm involvement, as carried out for fruit trees in west and southern Africa;
- A well-designed domestication program will include an exit strategy for all actors, both the farmers and their buyers. This exit strategy provides a route towards independence of all project actors after the project implementation period. Part of a well-designed program will be training in seed-collection practices, in order to prevent narrowing of the genetic base of subsequent *Jatropha* generations, and postharvest handling to ensure viability. Without such basic practices, selection for favorable traits, such as production, oil content and/or seed size, will not yield benefits. Selection may,

depending on the heritability of the selected traits, give an initial positive response due to selection of superior genotypes, but this positive effect could be lost in subsequent generations, due to a narrowing of the genetic base [55].

▪ Breeding strategies for larger commercial plantations

The breeding strategy for commercial plantations will, in its first steps, have similarities to the farmer-based domestication, with provenance testing in field trials in relevant environmental conditions and in agricultural systems similar to the systems that are expected to be applied in the plantations. The field trial testing of provenances and trees within provenances should be made simultaneously to identify superior oi-producing and climate-robust provenances and trees. The trees can be tested either as clones, (i.e., by ramets [cuttings] or by progeny) [16]. The clonal testing approach will make estimation of genetic values and, thus, selections more precise. This is of course of high relevance if plantations are to be established with clones. In the case that mass production through seed propagation is wanted, clonal testing is still an effective way to increase the certainty in the selections [95], unless large clonal effects and non-additive genetic effects weaken the correlations between estimated genetic values and breeding values. Mass production through seed propagation will require the establishment of seed orchards with the selected trees [16].

The number of clones used in the case of clonal propagation for deployment in the plantations depends on the expected rotation age of the plantations, degree of genotype by environment interaction, risks for new pests, the degree of genetic variation between clones and, finally, the willingness to accept risks to obtain high genetic gains. Thus, short rotation, low genotype by environment interaction, low risk for severe pests and large genetic variation between clones speak in favor of few clones. Additionally, the use of fewer clones will make it easier to obtain homogenous harvest properties [94].

The breeding strategies for commercial plantations will require a breeding program with crossings between selected genotypes, testing of offspring from the crosses and, finally, deployment of superior offspring through either clonal propagation or seed propagation in seed orchards [16]. To secure long-term genetic gains, the breeding program could be organized using the concept of multiple breeding populations [15,16], as discussed previously. If the species is mainly regenerating through apomixis, the generation of new variations in a breeding program will be more troublesome, and it may also increase the risk that the genetic variation between clones is actually small.

Conclusion

Information on most aspects related to breeding and domestication of *Jatropha curcas* is scarce. Only a limited number of studies have described *Jatropha* regeneration ecology or the genetic resources or diversity. Additionally, these studies are often made outside the natural distribution area of the species. The information available makes it possible to formulate hypotheses, but is rarely sufficiently detailed to confirm or dismiss these hypotheses.

Current knowledge warns for inbreeding depression, since *Jatropha*, an outcrosser needing pollinators, is also self-compatible. Low variation observed in markers within populations of *Jatropha* might confirm this or be an indication of a population structure with a high level of genetic homogeneity. It is important to confirm or reject the hypothesis of nonpanmictic breeding as it is central for domestication design. Several studies point towards low genomic diversity of *Jatropha* landraces, but insufficient information is available on the genetic diversity in the native gene pools. It is an interesting challenge to perform 'smart' outcrossing between superior individuals in Asian and African landraces with new introductions from Central America. This could be performed intraspecifically and interspecifically. However, sufficient knowledge concerning the genotype by environmental interaction is missing: genetic testing over a range of environments (provenance trials) is needed.

It must be acknowledged that *Jatropha* is suitable for quick and efficient domestication compared with other woody species and that much research is currently ongoing to fill the knowledge gaps. According to us, germplasm improvement should address:

- A further exploration of the genetic resources (certainly in the native gene pools);
- In-depth analysis of the *Jatropha* breeding system together with apomixis;
- Determination of the effect of inbreeding and outbreeding.

Conventional breeding is suitable for selecting traits, such as seed yield, seed size and oil yield, but also for developing planting material adapted to local environmental conditions. A clone-based breeding approach could be interesting for *Jatropha* as well, certainly when the indication of apomixis in *Jatropha* can be confirmed. Molecular-assisted breeding and transgenetic approaches are mainly of interest to develop nontoxic genotypes.

There is a growing body of knowledge in support of agroforestry for future ecoagriculture, farm diversification and management of climate change in the tropics. *Jatropha* is suitable for integration in different agroforestry systems. In this sense, *Jatropha's* domestication can provide a powerful means of socioeconomic management involving income generation, climate change mitigation, soft farming and sustainable development. Therefore, *Jatropha* domestication should be farmer-centered and market-led, involving the careful participatory selection of the species' traits to be addressed by breeding and elite cultivars adapted to the local environmental conditions. The domestication strategies should be simple and developed in cooperation with farmers.

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Executive summary

Regeneration ecology

- *Jatropha* is an outcrosser that is self-compatible and needs pollinators.
- The mechanism that balances the promotion of outcrossing and minimizes self-pollination is poorly understood.

Genetic resources, diversity & characterization of breeding systems

- Preliminary studies indicate very low levels of marker polymorphism within populations of *Jatropha,* even in its natural range.
- It is important to confirm or reject the hypothesis of nonpanmictic breeding, as it is central for domestication design.
- Several studies point towards low genomic diversity of *Jatropha* landraces, but the role of inbreeding depression in *Jatropha* landraces remains uninvestigated.
- The genetic diversity in the native gene pools (center of origin) stays largely undiscovered.
- 'Smart' intraspecific and interspecific crossing between superior individuals in Asian and African landraces with new introductions from Americas will be needed to increase the genetic pool of *Jatropha* accessions.

Seed source tests & development of varieties

- There is a clear need for more genetic seed source tests over a range of environments to reveal possible genotype–environment interactions (provenance trials).
- Breeding for nontoxic *Jatropha* varieties with low levels of phorbol esters provides promising prospects.

The route to better germplasm

- Comparing *Jatropha* to other species of Euphorbiaceae will be suitable to help in the process of domestication.
- Necessary steps to take on the route to better germplasm:
  - Further exploration of the genetic resources available
  - Thorough analysis of the *Jatropha* breeding system
  - Determination of the effect of inbreeding and outbreeding
- Breeding options consist of conventional breeding, molecular breeding and transgenetic approaches. Where the latter two show most opportunities for the development of nontoxic genotypes, conventional breeding selects for higher seed yields, seed size and oil yield.

Future perspective

- We believe that integrating *Jatropha* into existing smallholder agroforestry systems through participatory domestication strategies can form a robust and sustainable base for *Jatropha* domestication and sustainable development.
- Farmers and scientists need to domesticate *Jatropha* together in the framework of agroforestry.

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