Global maximization of *Jatropha* oil production under semi-arid conditions by balancing vegetative growth with reproductive capacity

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Abstract

*Jatropha curcas* L. is a drought tolerant crop that is globally cultivated under semi-arid conditions as a biodiesel feedstock. Despite its great potential, however, many projects failed to reach commercially viable seed and oil yields. The aim of the study was to provide globally applicable solutions for maximization of *Jatropha* oil production under semi-arid conditions. Under extremely low irrigation (10% of potential evapotranspiration; ETp), fruit production was very low and a surprisingly significant portion of the fruits delayed their maturity up to six months post-bloom. Increasing irrigation to mid-level (60% ETp) significantly elevated fruit production and speeded up the ripening rate, whereas further increasing irrigation to a higher level (90% ETp) decreased seed and oil yields, probably due to the increased investment in vegetative growth. Nevertheless, maximal seed and oil yields at 60% ETp remained far below targeted yields. Coupling irrigation at 60% ETp, with induction of vegetative arrest, by soil application of a commercial gibberellin synthesis inhibitor, brought forward the second bloom period by two months, reduced vegetative growth, promoted floral production and significantly enhanced reproductive capacity by more than doubling oil production. The results show that under semi-arid conditions, commercially viable seed and oil yields of *Jatropha* can be achieved by carefully balancing vegetative growth with reproductive capacity through the combined application of optimal irrigation regimes and induced vegetative arrest.

Keywords: biodiesel feedstock, bloom phenology, fatty acid composition, growth regulators, reproductive success, vegetative arrest

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Introduction

*Jatropha curcas* L. (*J. curcas*) is a small perennial tree of the Euphorbiaceae; native to the tropical and subtropical regions of Central America (Heller, 1996). The plant is monoecious with separate male and female flowers residing on the same bloom clusters (Raju & Ezradanam, 2002; Samra et al., 2013). The male flowers have ten stamens, while female flowers have three bifid stigmas and a three carpels ovary, to create a three-seeded green capsule, which later becomes yellow and finally a mature brown fruit (Raju & Ezradanam, 2002).

During the past two decades, researchers have attempted to explore *J. curcas* seed oil as feedstock for biodiesel (Foidl et al., 1996; Huerga et al., 2014). Seed and kernel oil concentrations of *J. curcas* vary from 30% to 50% and 45% to 60%, respectively (Pramanik, 2003). Seed-oil composition was found to be highly suitable for biodiesel as it is rich in unsaturated fatty acids (>72%), mainly oleic and linoleic fatty acids, followed by the saturated palmitic and stearic fatty acids, together accounting for >98% of the oil (Akintayo, 2004; Vaknin et al., 2011).

However, due to the plant’s relatively wild nature and the enormous gaps in knowledge about the its genetic background and optimized agronomic practices, many *J. curcas* projects failed to reach commercially viable yields (Sanderson, 2009; Kant & Wu, 2011; Singh et al., 2014; Edrisi et al., 2015; Vaknin et al., 2015b) and were subsequently abandoned.

Suitable zones for high *J. curcas* seed yields are located in both tropical and hot temperate areas with a preference to a strong or partial dry season (Trabucco et al., 2010). The minimum annual precipitation at which *J. curcas* was previously suggested to yield a
harvestable amount of seeds was 500–600 mm and optimal annual precipitation was suggested as 1000–1500 mm (Foidl et al., 1996; Henning, 2000; Achten et al., 2008; Behera et al., 2010). In permanently humid and hot regions, J. curcas will grow and bloom throughout the year (Heller, 1996), while in more seasonal, as in Mediterranean regions, it will bloom with two distinct peaks; during summer and autumn (Raju & Ezradanam, 2002; Wang & Ding, 2012; Y. Vaknin, 2017 personal information).

Jatropha curcas is well adapted to semi-arid conditions, prevalent in Mediterranean and adjacent desert climates, and is therefore considered to be drought tolerant (Rijssenbeek, 2007; Abou Kheira & Atta, 2009; Makkar & Becker, 2009; Sanderson, 2009; Parawira, 2010; Siddharth & Sharma, 2010; Díaz-López et al., 2012; Sapeta et al., 2013). Under such conditions, the plants shed their leaves, and seed and oil production are dramatically reduced (Openshaw, 2000; Prueksakorn & Gheewala, 2008)

The primary goal of growers and commercial companies was to enhance reproductive capacity and yielding potential of J. curcas with minimal targeted yields ranging between 2000 and 5000 kg seeds per hectare (Daniel, 2008; Brittaine & Lutaladio, 2010; Yang et al., 2010; Sims, 2012; Singh et al., 2014; Y. Vaknin, 2017 personal information). To reach that goal, several agro-technologies were practiced globally:

1. optimal irrigation and fertilization was suggested to help widen the area suitable to J. curcas to include regions that are more arid, thus, mitigate climatic stresses and increase seed and oil yield (Jongschaap et al., 2007; Achten et al., 2008; Maes et al., 2009; Trabucco et al., 2010). Most studies focused on the vegetative aspects of J. curcas growth and development (Maes et al., 2009; Achten et al., 2010; Behera et al., 2010; Al-Busaidi et al., 2012; Díaz-López et al., 2012; De Miguel et al., 2013; Yang et al., 2013; Dorta-Santos et al., 2014). Thus, supplementary irrigation of J. curcas was determined to be essential for the enhancement of vegetative growth as well as yield. However, increased irrigation levels were also found to induce biomass production at the expense of reproductive capacity (Rao, 2006; Ghosh et al., 2007; Achten et al., 2008). On the other hand, only a few studies tested the significance of irrigation for seed and oil productivity under semi-arid conditions (Abou Kheira & Atta, 2009; Tikkoo et al., 2013) and reached oil yields that were far below the minimal production goals (60 and 160 kg per hectare, respectively).

2. Pruning of J. curcas has become a common practice to shape the plants architecture at a young age of 6 to 12 months (Gour, 2006; Kureel, 2006; Reddy & Naole, 2009), and later at dormancy, to reduce plant height for easier harvest (Brittaine & Lutaladio, 2010) and promote branching which is highly associated with enhanced flowering and fruit and seed production (Gour, 2006; Kumar & Sharma, 2008). In most cases, however, increased seed and oil yields remained far below the minimal production goals. Furthermore, in non-irrigated hedge plantings, J. curcas seed yield was positively associated with plant height and number of productive branches. Their reported yields were also far below targeted levels (Tjeuw et al., 2015).

3. Various plant growth regulators were applied on J. curcas to enhance branching (Abdelgadir et al., 2009), reduce plant height (Ghosh et al., 2010; Xu et al., 2013), increase number of female flowers and increase yield (Babu et al., 2009; Abdelgadir et al., 2010; Ghosh et al., 2010; Makwana et al., 2010; Xu et al., 2013). In most studies, however, increased seed and oil yields remained far below the minimal production goals.

In the past 10 years, an attempt was made to maximize the potential of J. curcas as an oil crop under semi-arid conditions in the Israeli coastal plains and in the northern Negev desert, with mean annual precipitation of 300–500 and 100–200 mm, respectively (Israel Meteorological Service). Both vegetative growth and reproductive success were significantly affected by such conditions (Vaknin et al., 2015b): Two-year-old plants exposed to decreasing levels of irrigation, from 100% to 10% ETp, showed a similar number of newly emerging branches after winter pruning, at all irrigation levels. However, the number of flowers per plant and fruit and seed sets and seed-oil contents were significantly reduced with decreasing levels of irrigation, at both summer and autumn bloom periods. Typically, the summer bloom period was more prolonged with most fruits failing to mature and produce harvestable seeds, due to the nearing cold winter, and thus, a great part of the reproductive potential was lost (Y. Vaknin, 2017 personal information). Additionally, while recording fruit and seed production (Samra et al., 2013; Samocha et al., 2014; Vaknin et al., 2015a), smaller fruits were encountered, which were often dismissed as aborted. Close inspection revealed that a significant portion of these non-developed fruits gradually matured and ripened over the course of the next six months. The research hypothesis was that this unique pattern of partially delayed fruit ripening (PDFR) was primarily associated with the adverse conditions of the hot and dry conditions during summer.

The aim of the current study was to maximize the reproductive potential (i.e., production of female flowers) and reproductive capacity (i.e., production of fruits and seeds) of J. curcas, in order to reach commercially
viable seed and oil yields, under semi-arid conditions. By combining several agro-technologies, primarily irrigation, pruning and a plant growth regulator, an attempt was made to elucidate the significance of irrigation and vegetative growth for mitigation of reduced seed production and PDFR and produce workable protocols with potential application in semi-arid regions worldwide.

Materials and methods

Study locations and plant material

The study was conducted at two locations, 85 Km apart: (i) The Volcani Center research institute in central Israel (31°59′N, 34°49′E); and (ii) Kibbutz Hazerim in the northern Negev desert (31°14′N, 34°42′E). Local climatic conditions of both locations were hot dry summers with cool and wet winters with an average annual precipitation of 524 and 195 mm, respectively (Israel Meteorological Service). At both locations, the three-year-old plants constituted a random mix of accessions collected from Brazil, China, Ethiopia, India, Mozambique, Niger and Suriname. Planting density was 3 × 2 m, and fertigation was applied via drip irrigation throughout the summer and early autumn (water mixed with NPK fertilizer, 20-20-20, 1 g per 10 l). Potential evapotranspiration (ETp) was calculated from meteorological data of a nearby station using a modified Penman-Monteith equation (Allen et al., 1998) and multiplied by a cover factor.

Bloom phenology, seed production and oil traits under semi-arid conditions

Bloom phenology of six three-year-old seedlings was documented on a weekly basis, in a 0.2 ha plot at the Volcani Center research institute, during June–December 2009, encompassing a full annual bloom period. Water availability was severely reduced (10% ETp) throughout the season. Collected data included the number of flowering inflorescences and number of male and female flowers per inflorescence, at a sample of five inflorescences per plant. The number of immature and mature fruits was noted on a weekly basis. Fully ripened fruits were harvested, and the number of seeds per fruit was counted.

Mature seeds were classified into four arbitrary groups (n = 15 per group): (i) Regular development at approximately 230 ordinal days (August 2009); (ii) Second ripening group at approximately 260 ordinal days (September 2009); (iii) Third ripening group at approximately 290 ordinal days (October 2009); (iv) Fourth ripening group at approximately 320 ordinal days (November 2009). Seeds and kernels were dried under room conditions, weighted and then scanned using the NIRS (Near Infrared Reflectance Spectroscopy) method that was developed by Vaknin et al. (2011) and calibrated for J. curcas, to provide a reliable estimation of concentrations of oil and the four major fatty acids; oleic, linoleic, palmitic and stearic.

The significance of irrigation for fruit production and PDFR

The significance of irrigation for PDFR was tested during 2010, at the Volcani Center research institute, in a 0.5 ha plot of 3-year-old seedlings arranged at a random two-block design with three treatments: (i) Low irrigation (10% ETp) throughout the summer (May–September); (ii) Low irrigation (10% ETp) for two months (May–June) followed by mid irrigation for the remainder of the summer (60% ETp; July–September); and (iii) Mid irrigation (60% ETp) throughout the summer (May–September). In late August, the entire fruit load of five random trees, per treatment, per block (n = 10) was harvested; the fruits were counted; and their level of maturity was noted.

Statistical analyses

Statistical analyses were performed with JMP 12.0.1 software (SAS Institute Inc. Cary, NC, USA) according to Sokal & Rohlf (1995). T-test was used to analyze the effect of first and second bloom periods on phenological traits and to compare the number of seeds per fruit between normally developed fruits and delayed ones. One-way analysis of variance (ANOVA) was used to compare different periods of fruit maturation on seed traits and fruit counts under different levels of irrigation. Post hoc Tukey–Kramer HSD was performed on all
ANOVA analyses. One-way analysis of variance (ANOVA) was also used to compare between nine different treatments of irrigation combined with vegetative arrest on values of the number of old and new branches, the number of female flowers and the number of seeds per tree, adjusted for the fact that the results came from the same blocks. A full factorial ANOVA was performed to test the separate effects of irrigation and vegetative arrest on the performance of the plants as well as their potential interaction. Square-root and arcsine square-root transformations were applied to counts and percentages, respectively. All data are represented as the mean ± standard error. Values are reported as significantly different if $P < 0.05$.

**Results**

**Phenological traits under semi-arid conditions**

*Jatropha curcas* bloom was characterized by two major periods; the first, during spring and early summer (June–July), was short with a high male to female flower ratio compared to the more extended second period that spanned throughout the entire autumn until early winter (October–December) (Fig. 1a). Number of inflorescences per tree was similar for both periods ($P = 0.5059$, $n = 6$). The first bloom period, however, was characterized by a significantly ($P < 0.0001$) lower number of female flowers per inflorescence (3.58 ± 0.22, $n = 268$), in comparison with the second one (7.55 ± 0.33, $n = 180$).

In summer of 2009, under severely reduced water availability (10% ETp), a novel phenomenon of PDFR was documented: While some fruits reached maturity approximately two months after flower anthesis (Fig. 1b), others showed a significant delay in their development of up to six months. These fruits remained green and relatively small (~5 mm) and they gradually matured, in four periods, over the course of the next six months (I – IV; Fig. 1b). Nearly 30% of the fruits showed some delay of delay in their development ($n = 173$) with 70% of the delayed fruits initiating maturation in mid-August (~230 ordinal days, Fig. 1b) and 65% reaching full maturity by early winter. Number of seeds per fruit was significantly higher for regularly developed fruits ($P < 0.0001$) (2.31 ± 0.02, $n = 437$) compared to delayed ones (2.62 ± 0.02, $n = 149$).

Significant differences were found between seeds of four distinct ripening periods I, II, III and IV (Table 1): Both seed and kernel weights were lower for fruits from the fourth ripening group (IV), as opposed to seeds from fruits that ripened earlier (periods I, II and III). Kernel oil concentration from the fourth ripening group was significantly higher than from earlier ripening fruits while seed-oil content remained constant throughout the extended ripening period (Table 1). As ripening was delayed, the concentration of palmitic, stearic and oleic acids in the oil significantly decreased, while the one for linoleic acid was increased (Table 1).

The significance of irrigation for fruit production and PDFR

The significance of irrigation for fruit production and PDFR was tested under several irrigation regimes (Table 1). Fruit production of low irrigated trees (10% ETp) was significantly lower than that of trees that received mid-level irrigation (60% ETp) throughout the experiment and trees that were initially low irrigated and later received mid-level irrigation (35.4 ± 8.1, 47.4 ± 8.44, 68.0 ± 9.20 fruits per plant, respectively).

Trees irrigated at 10% ETp produced the highest percentage of delayed fruits (24.0 ± 5.55) in comparison with trees that initially received 10% ETp and later 60% ETp (7.0 ± 1.85) and trees that received 60% ETp throughout the experiment (0.6 ± 0.39) (Fig. 2). In late summer (August), fully developed fruits were most abundant in trees that initially received 10% ETp and later 60% ETp (68.8 ± 7.47%) than trees that were irrigated at 60% ETp (53.6 ± 9.29%) or 10% ETp (37.6 ± 6.58%) throughout the experiment (Fig. 2).

The significance of irrigation, coupled with vegetative arrest, for seed and oil production

The trees, under three levels of irrigation, combined with three treatments of vegetative arrest, initiated growth in late spring by producing new branches from the ones that were pruned the previous winter. Both number of old and new branches were significantly affected by irradiation level, while vegetative arrest had no such effect. Trees, receiving 30 and 60% ETp had a similar number of branches and trees receiving 90% had a slightly lower number of branches (Fig. 3a). By mid-summer, the number of branches for trees receiving 30 and 60% ETp was nearly doubled while that for 90% ETp was more than doubled, thus nearly reaching a similar number of branches per tree (Fig. 3a).

Maximal plant height, on the other hand, was significantly affected both by irrigation level and vegetative arrest. It was further enhanced by the combined interaction between the two treatments suggesting that the effects of irrigation level differ for the different treatments of vegetative arrest. Plant height increased linearly with increasing levels of irrigation from 250 to 300 and 350 cm under 30%, 60% and 90% ETp, respectively (Fig. 3b). When the treatments of vegetative restriction were applied, plant height was significantly reduced...
under all irrigation levels. However, while both treatments of vegetative restriction similarly reduced plant height under 30% ETp, with increasing levels of irrigation, the treatment of additional pruning became more effective in reduction of plant height than soil application of uniconazole (Fig. 3b).

The number of female flowers and the number of seeds per tree for three consecutive bloom periods, in the same season, is presented in Fig. 4a–c:

1. First bloom period occurred in early summer (Fig. 4a). During that period, trees irrigated at 30% ETp produced the least amount of female flowers and seeds, while trees irrigated at 60% ETp produced the highest amount of female flowers and seeds. Increasing irrigation to 90% ETp resulted in a modest decrease in flower and seed production compared to 60% ETp. Both measured traits were significantly affected by irrigation level, while vegetative arrest had no such effect.

Fig. 1 Bloom phenology and fruit production of six *Jatropha curcas* plants under Mediterranean semi-arid conditions at the Volcani Center research institute, during June–December 2009. (a) Number of viable male (red full circles) and female (blue full squares) flowers, during summer and autumn bloom periods. (b) Number of delayed fruits (green full squares) and number of fully ripened mature fruits (brown full circles), originating from the summer bloom period in four (I–IV) periods.

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Table 1  Comparative analyses of seed and kernel weight, oil concentration, and content in the kernel, protein concentration, and content in the kernel, oleic, linoleic, palmitic, and stearic acid concentrations in the oil obtained from four ripening groups in 2009 at the Volcani Center research institute: Ripening group I (August), Ripening group II (September), Ripening group III (October), and Ripening group IV (November)

| Variable            | Ripening group I | Ripening group II | Ripening group III | Ripening group IV | Significance |
|---------------------|------------------|-------------------|--------------------|-------------------|--------------|
| Seed weight (g)     | 0.59 ± 0.02 ab   | 0.62 ± 0.01 a     | 0.58 ± 0.03 ab     | 0.52 ± 0.02 b     | *            |
| Kernel weight (g)   | 0.37 ± 0.01 ab   | 0.40 ± 0.01 a     | 0.37 ± 0.02 ab     | 0.33 ± 0.02 b     | *            |
| Oil Concentration (%) | 50.84 ± 0.73 b  | 54.81 ± 0.83 ab   | 57.38 ± 1.59 a     | 56.08 ± 1.95 a    | **           |
| Oil Content (g)     | 0.19 ± 0.008     | 0.22 ± 0.005      | 0.21 ± 0.013       | 0.19 ± 0.013      | n.s          |
| Fatty acids (%)     |                  |                   |                    |                   |              |
| Palmitic (C16:0)    | 13.42 ± 0.16 a   | 13.11 ± 0.12 ab   | 12.55 ± 0.22 b     | 12.72 ± 0.27 b    | *            |
| Stearic (C18:0)     | 6.81 ± 0.15 a    | 6.78 ± 0.17 a     | 6.35 ± 0.12 ab     | 5.87 ± 0.16 b     | ***          |
| Oleic (C18:1)       | 42.21 ± 1.07 a   | 42.40 ± 0.72 a    | 38.76 ± 1.51 ab    | 38.26 ± 1.04 b    | *            |
| Linoleic (C18:2)    | 31.74 ± 0.87 c   | 33.39 ± 0.73 bc   | 36.22 ± 1.52 ab    | 38.77 ± 1.01 a    | ***          |

All data are shown as means ± SE. Means marked with the same letter are not significantly different according to Tukey–Kramer HSD. n.s, non-significance; *P < 0.05; **P < 0.01; ***P < 0.001.

2. Early second bloom period occurred in late summer, nearly two months prior to the regular second bloom period (Fig. 4b). Control trees, as well as trees that were additionally pruned, produced very little if any flowers and seeds at all three irrigation levels. Uniconazole application, however, resulted in an enormous increase in production of female flowers and seeds at all irrigation levels with the highest production at 60% ETp and the lowest production at 90% ETp. Both measured traits were significantly affected by the treatments of vegetative arrest, while irrigation level had no such effect.

3. Regular second bloom period occurred in autumn (Fig. 4c). Control trees showed a regular pattern of bloom with the highest number of female flowers and seeds at 60% ETp and the lowest numbers at 30% ETp. Trees that received either treatment of vegetative restriction produced very little if any flowers and seeds at all three irrigation levels. Both measured traits were significantly affected by both treatments of irrigation level and vegetative arrest, and the significant interaction between the two suggests that the effects of irrigation level differ for the different treatments of vegetative arrest.

Calculating seed and oil production from the above-mentioned three bloom periods, resulted in estimated seed and oil yields for all nine treatments (Fig. 5): Control trees subjected only to 60% ETp produced nearly 2000 kg ha\(^{-1}\) yr\(^{-1}\), while the remaining control trees and trees that were additionally pruned produced significantly lower yields ranging at approximately 100–1000 kg ha\(^{-1}\) yr\(^{-1}\). Trees subjected to uniconazole vegetative arrest produced the highest yields under all three irrigation levels, with seed yields of above 5000, 4000 and 3000 kg ha\(^{-1}\) yr\(^{-1}\) for trees irrigated at 60%, 30% and 90% ETp, respectively.

Discussion

Phenological traits under semi-arid conditions

Environmental conditions affect both bloom phenology as well as fruit production of terrestrial plants (Rathcke & Lacey, 1985). Under semi-arid conditions, J. curcas bloomed both in summer and in autumn, with the second period accounting for approximately two-thirds of the reproductive potential (i.e., the number of female flowers). Realizing this reproductive potential as viable harvestable seeds, however, is very problematic as most fruits fail to mature during the nearing cold winter. Production of harvestable seeds from the first bloom period is also problematic as it accounts for only a third of the reproductive potential and is highly dependent on sufficient amounts of irrigation and fertilization, which are, yet to be determined.

Extremely low irrigated plants (10% ETp) cope with these harsh conditions by spreading out the ripening period from a few weeks up to six months, at four consecutive ripening periods, thus making commercial harvest nearly impossible. Here we propose this unique phenomenon of PDFR as a resource management strategy to increase reproductive capacity under physiological stress. Nevertheless, this pattern of delayed development was slightly detrimental to seed production per fruit, as well as seed size. Seed-oil content, however, remained constant throughout the extended ripening period (Table 1) probably as reduced seed weight in the fourth ripening period was ‘compensated’ by increased oil concentration.

Post-floral conditions are known to significantly affect seed traits. Low temperature during the period of fruit development has been reported to be the cause for biochemical differences that can influence, among
other things, oil content (Wolf et al., 1982; Rathcke & Lacey, 1985). The concentration of palmitic stearic and oleic acids decreased significantly with delayed ripening, while the concentration of linoleic acid was increased. This decrease in oleic acid and increase in linoleic acid is directly associated with synthesis of linoleic acid by a desaturation reaction on oleic acid, its precursor, which introduces an additional double bond into the fatty acyl chain (Yuan & Bloch, 1961; Nelson and Cox 2000). In the current study, the most significant changes in fatty acid concentrations occurred during the third ripening period, which directly coincided with the onset of autumn, and a significant reduction in ambient temperatures. Harris & James (1969) described one mechanism for this phenomenon suggesting that in no-photosynthetic tissue with a fixed activity of desaturase enzymes, oxygen was the major rate-limiting factor of desaturation of fatty acids. As solubility of oxygen increases with reduced temperature, it is directly reflected in the increase in the desaturation of the fatty acids. In accordance with our results, Wolf et al. (1982) found that in soybean plants, grown under low temperatures, oleic acid concentration decreased as linoleic acid concentration increased. Lanna et al. (2005) studied this phenomenon in the synthesis of oil in the seeds of soybeans and also found it to be highly influenced by environmental conditions; primarily temperature. They showed that in seeds produced under low temperatures, the enzymes
responsible for the desaturation of the fatty acids were more active.

The significance of irrigation for fruit production and PDFR

The strong conviction that *J. curcas* can be productive under semi-arid conditions with limited water availability and no irrigation has led to the failure of many projects (Contran et al., 2013). In the current study, fruit production of low irrigated trees (35.40/C6/8.08) was significantly lower than that of low irrigated trees followed by mid-levels of irrigation (68.00/C6/9.20) suggesting that not only was fruit development being retarded, but also reproductive capacity was reduced. Interestingly, mid-level irrigated trees were characterized by lower levels of fruit production (47.40/C6/8.44) compared with trees that were initially low irrigated and later received mid-level irrigation. The results suggest that the plants partly delayed the development of their fruits, until water availability was increased, and only then, began to advance their development toward full ripening. While the plants were exposed to low levels of irrigation, their vegetative growth was minimal, but their reproductive potential (i.e., production of female flower buds) was elevated probably as higher levels of irrigation promoted extensive vegetative growth at the expense of reproductive success.

A prolonged period of seed development was also documented in some conifers, where fertilization occurs...
one year following pollination, while seed maturation takes additional 15–18 months (Owens & Molder, 1977; Owens et al., 1995). These examples, however, describe constant obligatory developmental periods and are thus essentially different from findings of the current study. In the animal kingdom, delayed embryo development due to reduced availability of resources is a known phenomenon as in the case of roe deer (Capreolus capreolus) (Aitken, 1974; Sandell, 1990).

The significance of irrigation, coupled with vegetative arrest, for seed and oil production

The results support the claim that under semi-arid conditions, supplementary irrigation of J. curcas is essential to achieve harvestable yield, however, increased irrigation may induce enhanced biomass production at the expense of reproductive success (Ghosh et al., 2007). Reproductive potential and reproductive success during the summer and autumn bloom periods, presented here as number of female flowers and number of seeds (Fig. 4a, c), respectively, were maximal under mid-level irrigation (60% ETp) and lowest under 30% ETp, probably as increasing irrigation to 90% ETp promoted vegetative growth at the expense of reproductive capacity.

Uniconazole and paclobutrazol are members of the gibberellin antagonist family and are both regularly applied on a variety of horticultural crops (Davis et al., 1988; Dag et al., 2006; Avidan et al., 2011; Schneider et al., 2012) to reduce vegetative growth and increase fruit production through improved floral induction and reduced competition with vegetative growth. Previously, paclobutrazol was applied on J. curcas without alteration of irrigation levels in Gujarat India, under 882-mm annual precipitation (Ghosh et al., 2010) and in Guizhou province, China, under 1010 mm annual precipitation (Xu et al., 2013). Both studies resulted in inhibition of vegetative growth and enhancement of reproductive success, but maximal recorded yields were far below targeted commercial ones and agro-technological protocols could not be replicated elsewhere.

A comprehensive study conducted in India, on various climatic conditions, testing, separately, three agrotechnologies; pruning, irrigation and fertilization, and spacing (Singh et al., 2013), revealed that J. curcas best performed under semi-arid conditions and close spacing of 2 x 2 m. Maximal seed yield of 1400 kg per hectare, however, remained below minimal targeted ones, described above. In the current study, coupling irrigation with induced vegetative arrest was aimed at increasing reproductive capacity under semi-arid conditions without the negative effects of enhanced growth. Both additional pruning and uniconazole application had a dwarfing effect under all levels of irrigation and most significantly under low irrigation (30% ETp). Additional pruning slightly brought forward the second bloom period under 30% ETp (Fig. 4b), but it had no effect on increasing annual seed and oil yields (Fig. 5). The most dramatic effects on bloom and yield resulted from the uniconazole application. It had brought forward the second bloom period by nearly two months, from autumn to late summer, thus allowing the seeds to fully mature. It also had a tremendous effect on bloom enhancement resulting in approximately 10-, three- and fourfold increases in reproductive success under 30, 60 and 90% ETp, respectively. While control, mid-level irrigated trees, performed best yet barely reached targeted yields, all uniconazole treated trees performed significantly better, reaching commercially viable yields, with maximal yields at mid-level irrigation. Low-level irrigation, which normally resulted in very low seed and oil production, was second only to the best performing treatment, suggesting that when uniconazole was applied, reproductive success was also elevated through growth inhibition and bloom enhancement. Thus, the combined effects of reduced investment in vegetative growth due to mid-level irrigation levels with hormonally induced reduction in vegetative growth and bloom enhancement resulted in maximal productivity under semi-arid conditions.

In conclusion, the current study provides a globally applicable agro-technological framework for J. curcas growers, under semi-arid conditions. This proposed methodology could be duplicated in other semi-arid regions by combining induced vegetative arrest with similar levels of irrigation, corresponding to the locally measured ETp, thus potentially revitalizing this crop as a commercially viable feedstock for biodiesel production. Genetic improvement of local varieties for enhanced seed production, which is highly correlated with oil production (Martin & Montes, 2015), should also be incorporated, further increasing oil yields.

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