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Full Length Article

Influence of the Amount of Sunlight on the Development and Flowering of *Jatropha curcas*

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Abstract

Jatropha curcas L. shows tolerance to long periods of drought and low soil fertility however, the amount of radiant energy of the sun, required for the development and production of fruits, is unknown. The objective of this study was to determine the effect of the amount of sunlight on the development and flowering of Jatropha. The plants were grown at 100, 90, 70 and 50% solar irradiance (SI). The heights and stem perimeters obtained were 95.25 and 28.45% greater for those developed at 30 and 50% SI. Those developed at 100 and 90% SI had 69.63% more branches and 46.85% more leaves. The amount of chlorophyll (SPAD) was higher in plants grown at 100 and 90% SI. For plants grown at 100 and 90% SI, flowering started at weeks 27 and 29, respectively, whereas, in the rest, it started after 44. Only 18.75% of plants with 0% shade did not produce inflorescences. There was an inverse relationship between SI and the height of the plant. The relationship between SI and flowering was inverse as well. In conclusion, SI is a factor that modifies the development of Jatropha and limits its flowering. In the latter sense, is required at least 1,600 µmol m^{-2} s^{-1} for proper flowering. © 2018 Friends Science Publishers

Keywords: Solar irradiance; Plant height; Stem diameter; Branches; Flowering time

Introduction

The radiant energy of the sun is one of the leading climatic factors that influence the development, survival, and reproduction of plants. The most significant amount of knowledge about the role of light in the germination, growth and flowering of plants, has been obtained from *Arabidopsis thaliana* (Folta and Maruhnich, 2007; Brouwer *et al*., 2012; Tian *et al*., 2017). In annual cycle plants as, *Aptenia cordifolia* (Arboleda, 2011), *Limonium* sp. (Posada and Moreno 2007), *Solanum lycopersicum* (Suyanto *et al*., 2012) and *Trifolium repens* (An and Shangguan, 2009), the effect of the amount of radiant energy on the development and production of flowers has confirmed the observations made in *A. thaliana*. At a low rate of radiant energy, the biomass of the plant and the speed of photosynthesis decrease, while the height of the plant increases. The flowering of the plants also depends on the photoperiod and the light intensity and quality (Folta and Maruhnich, 2007). In perennial plants, scarce is the work regarding the influence of light intensity, on germination, development, and flowering.

Jatropha is a perennial shrub that, under conditions of the humid tropics, develops and flowers in the first year after germination of the seed (Rincón-Rabanales *et al*., 2016). This plant can grow on marginal soils under different climatic conditions (King *et al*., 2009) and, once established; it is tolerant to water limitation. (Abou-Kheira and Atta, 2009; Ovando-Medina *et al*., 2009; Divakara *et al*., 2010). The flowering of Jatropha is asynchronous (Xu *et al*., 2012), and the frequency and quantity of flowers depend on the genotype and agro-climatic conditions however of the development of the plant, scarce is the knowledge (Costa *et al*., 2016).

Regardless of the genotype used to establish Jatropha plantations under diverse agro climatic conditions, it is possible that the differential development, flowering and seed production (Zhang *et al*., 2011; Sosa-Segura *et al*., 2012; Tewfik *et al*., 2012; Cañadas-López *et al*., 2017) can be a reflection of the quantity and quality of radiant energy received. For the above, the objective of this work was to determine the effect of the amount of sun light on the development and flowering of JatrophaMAP-08.

Materials and Methods

Biological Material

Mature seeds (500) were collected from Jatropha MAP-08 of the Jatropha Germplasm Bank of the Instituto de Biociencias of the Universidad Autónoma de Chiapas (14° 49' 45.45'' N, 92° 17' 45.54" O, 58 masl).

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Germination and Potting Transplant

Seed germination was carried out in black plastic trays (980 × 400 × 100 mm) containing Peat Moss substrate (Premier®, Mexico) in shade (90% black shadow mesh) and high humidity. Of the seedlings that emerged quasi-synchronically, 64 were selected. After two weeks of development, the seedlings had two expanded cotyledonal leaves and a stem approximately 15 cm in length. Under the previously mentioned conditions, the seedlings were individually transplanted to 20 L plastic pots (30 cm diameter, 35 cm depth). A mixture of sandy loam soil and vermicompost was used as substrate, in a ratio of 19:1 w/w (0.1% N). The pots were randomized into groups of 16 individuals (four groups), in 4 X 4 arrays, with a 2 m separation between them in an area of 10 m x 10 m per group (100 m^2). All seedlings were kept in full sunlight until the development of the first two true leaves.

Determination of the Amount of Solar Irradiance

To determine the amount of solar irradiance (SI) a pyrometer was used (Brand: Quantum Meter®, Model: LQS-QM). At 12:00 han average SI of 1809 µmol m^{-2} s^{-1} was obtained.

Treatment Design

According to the maximum of solar irradiance, four treatments were established: 1) 100% solar irradiance (SI-100) or 0% shade, 2) 90% solar irradiance or 10% shade (SI-90), 3) 70% solar irradiance or 30% shade (SI-70) and 50% solar irradiance or 50% shade (SI-50). To achieve the amounts of shade required, different types of shade mesh were used. Using the mesh previously mentioned, shade houses measuring 10 m x 10 m x 2.8 m were built. The work period was from March 11, 2014 to May 15, 2015. Shade houses were randomly placed in an area of 30 x 30 m at the experimental site, and each plant was considered a repetition.

Plant Maintenance

Water was added to each pot to field capacity whenever it was required.

Response Variables

The following variables were evaluated every 7 days after the first two true leaves, for 60 weeks: height (cm, by using measuring tape from ground level to the apex of main stem), steam perimeter (calculated from diameter (cm), by using digital callipers at 2 cm from ground level), number of leaves (by direct counting), number of branches (by direct counting), concentration of "chlorophyll" (with a Chlorophyll meter SPAD-502), weeks at flowering (direct count), number of inflorescences and duration of inflorescence (direct count).

Data Analysis

The data obtained from all variables were processed using analysis of variance ($\alpha = 0.05$) and subsequent comparison by means of the Tukey test ($\alpha = 0.05$). To clarify the behaviour of the height and perimeter of the plants relative to the amount of light received, a ratio between both variables was established and data underwent the t test under Ho: $\mu = \mu_0$ and bilateral p. Similar information management was followed for plant height and leaves quantity data. Statistical analysis was performed with *InfoStat Profesional 2011* software.

Results

In Fig. 1, the dynamics of growth of MAP-08 *J. curcas* plants, subjected to different levels of solar irradiance, is shown. In general, two stages were observed, characterized by the growth rate: the first during the initial 22 weeks of cultivation and the second from week 23 to week 60 of evaluation. In the first stage, the average growth rate (cm $week^{-1}$) was 2.04, 2.60, 2.98, and 3.48 for the SI-100, SI-90, SI-70, and SI-50 treatments; in the second stage, speed, for the same treatments, was 0.60, 0.29, 0.41, and 0.54.

During period of the study, the average height gains of SI-100, SI-90, SI-70, and SI-50 treatments were 72.3, 75.4, 86.5, and 104.0 cm, respectively. Differences in height were significant (df= 3; MS = 149969.21; F = 991.92; p = <0.0001; SEM = 0.4). During the first stage of growth, height gain using the same treatments resulted in 59.5, 79.2, 75.9, and 73.6% of the total height respectively. Both height gain and growth speed of the first stage were inversely proportional to the intensity of solar irradiance (Fig. 2).

Moreover, the dynamics of development of the main stem of *J. curcas* (Fig. 1) showed three stages: the first in weeks 0–8, the second from week 9 to 14, and the third from week 15 to 60. In the second stage, the highest average speed in perimeter gain was found; values obtained were 1.71, 1.66, 1.66, and 1.54 cm $week^{-1}$ for treatments SI100, SI90, SI70, and SI50, respectively.

During the whole period of the study, the average gain in perimeter was 32.4, 31.4, 29.0, and 27.9 cm $week^{-1}$ for treatments SI-50, SI-70, SI-90, and SI-100, respectively. Differences in perimeter were significant (df= 3, MS = 4267.71, F = 641.84, p<0.0001; SEM = 0.08).

Using the data for height (Hp) and perimeter (Pp) of the plant, proportionality between both values was established (Hp/Pp). Fig. 2 shows the dynamics of this proportionality. Wave dynamics were strongly influenced by the higher gain phases, either in height or perimeter.

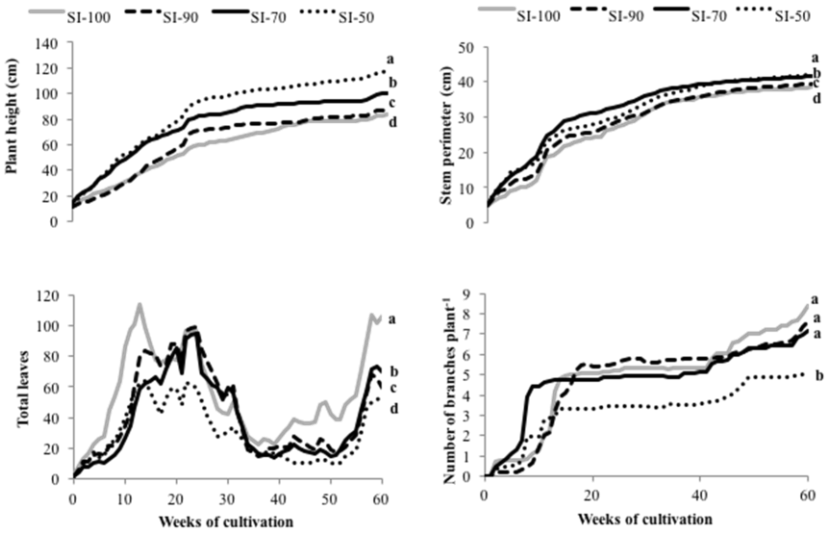

Fig. 1: Dynamics of plant height (above left), steam perimeter (above right), total leaves (down left) and number of branches (dawn right) of *Jatropha curcas* MAP-08 plants grown under different sunlight intensities (SI). The average values of each of the variables, and of the statistical descriptors, were written in the text. Treatments with equal letters had no significant difference at $p < 0.05$.

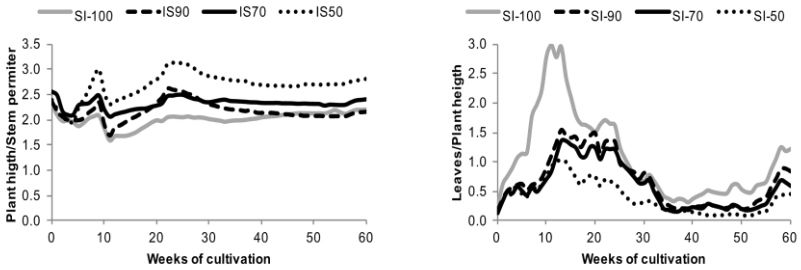

Fig. 2: Dynamics of relation plant height/perimeter of the main stem (left) and leaves/plant height (right) of Jatropha MAP-08 plants grown under different sunlight intensities. The significance of the values are shown in Table 1

Therefore, the first peak (week 9–10) coincided with the highest perimeter gain phase and the second peak (week 22–23) with the highest height gain.

Hp/Pp ratio for the SI-50 treatment had the highest mean value (2.67) of all treatments. The mean values of this relation for treatments SI-100, SI-90, and SI-70 were 2.01, 2.19, and 2.32, respectively. The t-test for the above data, under Ho: $\mu = \mu_0$, yielded p (bilateral) <0.0001 implied a difference between the average values of treatments (Table 1). Also, as SI increased, Hp/Pp ratio decreased linearly ($y = -0.0124x + 3.2559$; $r^2 = 0.96$).

With respect to the generation of secondary branches during the study period (Fig. 1), plants under SI-100 treatment produced, on average, 8.38 branches plant^{-1}. Plants under SI-50 treatment produced the least number of branches (4.94 branches plant^{-1}, on average).

The average production of branches in plants under SI-90 and SI-70 treatments was 7.50 and 7.23 branches a plant^{-1}, respectively. The dynamics of branch generation showed two phases whose duration was a function of the treatment. Between the first and second phases a dormant phase was exhibited, whose duration, on average, was 27 ± 2 weeks. The first phase ranged from week 0 to week 14, 18, 11, and 14, for treatments SI-100, SI-90, SI-70, and SI-50, respectively. The second phase started at week 41, 42, 40, and 41 for treatments SI-100, SI-90, SI-70, and SI-50, respectively, concluding at week 60, 60, 60, and 49 for the same treatments. It should be noted that for the SI-50 treatment, a second dormant phase was observed from week 49 until the conclusion of the study. Although we found a highly significant difference between treatments in ANOVA (df = 3, MS = 532.91, F = 240.09, $p < 0.0001$; SEM = 0.05), this was only between treatment IS50 and the rest, all of which were equal to each other.

With respect to the dynamics of leaf production (Fig. 1), a cyclical process was observed regardless of treatment. In this process, there was an increase in the number of leaves in the first phase, lasting from week 0 to weeks 10–13; afterwards, the number of leaves showed almost no change (for 12 to 13 weeks).

Table 1: Bilateralt-test for the Hp/Pp and L/Hp ratios of Jatropha MAP-08 plants, under the different SI treatments. n = weeks; MV =mean ratio value; LL = lower level of mean ratio value; UL = upper level of mean ratio value; t = value of tables

Treatment	n	MV	SD	LL (95)	UL (95)	t	p bilateral
Ph/Sp ratio							
IS-100	60	2.01	0.14	1.98	2.05	108.0	<0.0001
IS-90	60	2.18	0.19	2.13	2.23	90.7	<0.0001
IS-70	60	2.31	0.11	2.29	2.34	167.9	<0.0001
IS-50	60	2.67	0.26	2.61	2.74	80.8	<0.0001
L/pH ratio							
IS-100	60	1.07	0.74	0.88	1.26	11.3	<0.0001
IS-90	60	0.67	0.44	0.56	0.79	11.8	<0.0001
IS-70	60	0.59	0.39	0.49	0.69	11.9	<0.0001
IS-50	60	0.40	0.27	0.33	0.47	11.3	<0.0001

After the stabilization phase (of leaf numbers), a leaf decrease phase was observed, lasting 9 to 11 weeks, followed by a minimal quantity of leaves phase, lasting 17 to 19 weeks. Finally, a phase of increase in the number of leaves was observed again. In general, treatment SI50 showed the least amount of leaves, whereas treatment SI100 showed the most. Differences were significant (df = 3, MS = 106650.03, F = 425.22, P<0.0001). During the period of the study, the average of leaves plant^{-1}, by treatment, was 55.1 for SI-100, 42.74 for SI-70, 38.61 for SI-90 and 29.95 for SI-50 (df = 3, MS = 106650, F = 425.22, p<0.0001; SEM = 0.51). In general, no relationship between the amount of light received and the number of generated leaves plant^{-1} was found.

In order to better interpret the dynamics of plant height (Hp) and number of leaves (L), dynamics of the proportion L/Hp were constructed. Fig. 2 shows that the dynamics of this proportion was strongly influenced by the dynamics of the leaves. It was also observed that this proportion was always lower for plants under SI-50 treatment and higher for plants under SI-100 treatment. The mean values of L/Hp were 1.07, 0.67, 0.59, and 0.40, for SI-100, SI-90, SI-70, and SI-50, respectively. t-test of the above data, under Ho: $\mu = \mu_0$, yielded p (bilateral) <0.0001, implying a difference between the average values of treatments (Table 1). As SI increased, L/Hp ratio also increased. Such variation was adjusted to the linear relation ($y = 0.0117 x - 0.2173$; $r^2 = 0.83$).

On the other hand, the average value of the index of chlorophyll (SPAD units) for treatments SI-100 (35.9 SPAD) and S1-90 (35.6 SPAD) was statistically higher (df=3, MS = 264.96, F = 23.31 p<0.0001; SEM = 0.16) relative to treatments SI-70 (34.5 SPAD), and SI-50 (34.4 SPAD), and his dynamics were similar (Fig. 3).

With regard to flowering (Fig. 4), the plants under treatment with SI-100 had the first inflorescences 27 weeks after the start of the study, and the first inflorescences in the plants under treatment SI-90, appeared two weeks later. First inflorescences in plants under SI-70 treatment were observed at week 45, and at week 47 in plants under SI-50 treatment. Time required for inflorescence start showed a linear behaviour ($y = -0.439x + 70.271$; $r^2 = 0.90885$) as SI increased.

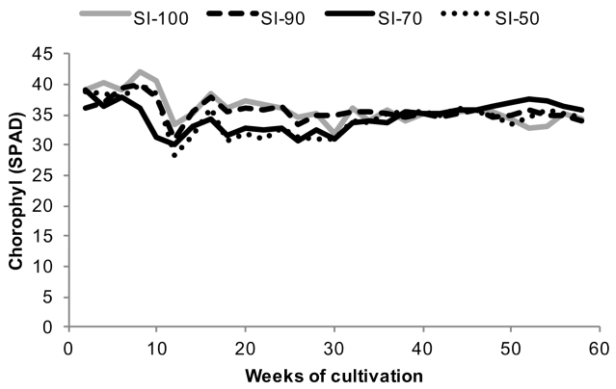

Fig. 3: Dynamics of chlorophyll (SPAD) of *Jatropha curcas* MAP-08 plants grown under different sunlight intensities (IS). The average values of each of the variables, and of the statistical descriptors, were written in the text

The dynamics of flowering (Fig. 4) showed that in the SI-100 treatment there was always a greater number of plants with inflorescence, whereas treatment SI-50 always had the smaller amount of flowering plants. At the end of the study, 81.25, 62.50, 43.75 and 43.75% of the plants under treatments SI-100, SI-90, SI-70, and SI-50, respectively, had inflorescences.

Discussion

It is widely documented that the amount, quality, direction, and duration of the light energy received by plants is a factor that determines their temporal and phenological development (De Lucas *et al*., 2008; Franklin and Quail, 2010; Kami *et al.*, 2010). Therefore, the height difference in plants subjected to SI-50 (+40.0% relative to plants subjected to SI-100 and SI-90, and +20.2% relative to SI-70) is a multifactorial response of light action. Among these we have the amount of indole-acetic acid (IAA) (Jones *et al*., 1991), its distribution along cells and stem (Jensen *et al*., 1998), and the induction and repression of genes (Casal and Yanovsky, 2005). Regarding the latter, it has been shown that, at low light intensity, many genes are repressed by phytochrome interacting factors (PIFs) (Galvão *et al*., 2012). Repression is eliminated when phytochromes A or B (Phy A or Phy B) are activated by far-red or red light, respectively [they change from the inactive form (Pr) to the active form (Pfr)], and degrade to PIF (Lorrain *et al*., 2008). The observed effect on the height of *J. curcas* MAP-08 higher to lower light intensity (Fig. 1), was similar to that reported in *Salvia officinalis* (Zervoudakis *et al*., 2012), sweet pepper (Stadler, 2010) and *Astenia cordifolia* (Arboleda, 2011).

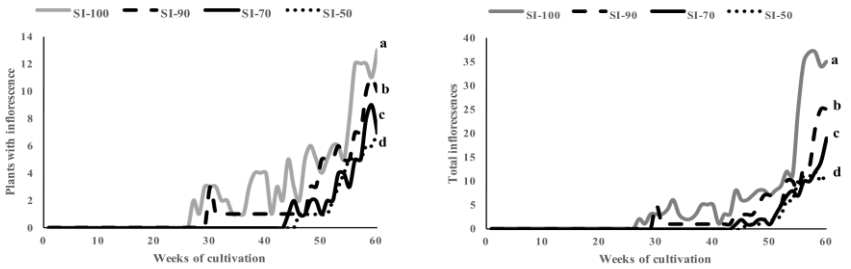

Fig. 4: Dynamics of the number of plants (left) and total inflorescences (right), of Jatropha MAP-08 plants with inflorescences, grown under different sunlight intensities (SI).The average values of each of the variables, and of the statistical descriptors, were written in the text. Treatments with equal letters had no significant difference at $p < 0.05$

On the other hand, the effect of light intensity on the perimeter of the stem (Fig. 1) was contrary to expectations, as smaller diameters are reported in plants grown with limited light intensity (Wassink and Stolwijk, 1956; Symons *et al*., 2008). The possible explanation is that in our work, all treatments started with seedlings that had at least two true leaves; that is, the photomorphogenesis program (Chen and Chory, 2011) was in progress and the amount of shade in treatments IS70 and IS50 was not sufficient to reverse it to the complete program of skotomorphogenesis. Thus, plants "feel" shade as the change in the red light/far-red light ratio; so that, at full sun the ratio is >1. When the shadow appears, the relation is <1 because there is an increase in red-distant light, reflected by the walls of the cells, and a fall in red light, absorbed by chlorophyll (Li *et al*., 2012). In Arabidopsis, prolonged shelter under shade triggers shade avoidance syndrome (SAS), whose symptoms are chlorophyll reduction, early flowering, low seed production and susceptibility to herbivory (Izaguirre *et al*., 2006). Likewise, Li *et al*. (2012) demonstrated that under shade, the greatest light sensor is phytochrome B, which is photoconverted into its inactive form (Pr) and is not associated with phosphorylated PIF-7; PIF-7 rapidly dephosphorylates and binds to the CACGTG sequence of the G-box regulating zone of the auxin synthesis genes, resulting in an increased concentration of free IAA. The excess of free IAA is transported towards the stem, causing the cells to elongate. Therefore, the largest increase in stem perimeter of plants under SI-70 and SI-50 treatments could be explained by the fact that the excess of IAA in such treatments caused elongation of the stem cells of *J. curcas.* Further studies should be conducted to determine which cells showed this symptom. The plant's height/perimeter ratio (Fig. 2) accentuates the phenomenon of overproduction of IAA (or growth hormones in general) when *J. curcas* plants are subjected, for a long time, to a shading process.

The mechanism described by Li *et al*. (2012) can also explain the behaviour of the generation of secondary branches for the different treatments of this study. At a higher shadow level (SI-50), there is higher IAA production and greater inhibition of axillary meristems. Considering the average number of branches counted after 60 weeks of cultivation, the inhibition level of shade treatments, SI-90, SI-70 and SI-50, was 9.3, 14.9 and 41.1%, respectively. Other forms of PIF are associated with the change in the architecture of the plant in the shade. Keller *et al*. (2011) reported that PIF-4 and PIF-5 were the factors involved in elongation of plant stems, and Franklin *et al*. (2011) reported that PIF-4 controls the expression of two genes for biosynthetic enzymes SAV3 and CYP79B, both of the auxin pathway.

Although the dynamics of leaf production under different shading treatments was similar (Fig. 1), their number was higher in plants under SI-100 treatment, indicating the effect of shading on this factor. The above may be the result of the presence of a greater amount of free IAA or the fact that some photochromic-PIF conjugate exerts negative regulation on the genes responsible for the organogenesis of leaves (regardless of the fact that development of dorsoventrally, the first stage of leaf formation, is dependent on regulation by microRNAs (Floyd and Bowman, 2004). Petiole elongation and the inhibition of leaf expansion (Franklin *et al*., 2003), symptoms derived from shading (Tsukaya, 2005), were not addressed in this study.

In spite of the difference in the number of leaves, photosynthetic capacity (Fig. 3) for treatments SI-70 and SI-50, was not lower, compared with treatments SI-100 and SI-90, in a single SPAD unit. This implies that chlorophyll biosynthesis was not affected by the 50% reduction of solar radiation. This result is opposite to that reported for *Arabidopsis thaliana* subjected to long periods of shade, where a decrease in chlorophyll content was reported (Izaguirre *et al*., 2006). This possible contradiction may be correlated with how the equipment measures the "content" of chlorophyll (it measures the transmittance of red and far-distant wavelengths and then transforms it into SPAD values). However, the SPAD meter yields a simple index, not the content or composition of the leaf pigments (Mielke *et al*., 2010).

The delay in the flowering of the plants subjected to shading can have several explanations. The soundest is that it could be associated with the concentration of glutathione (GSH), since it has been reported that in Arabidopsis, the

flowering time depends on the concentration of GSH. The synthesis of GSH is limited by the amount of ATP derived from photosystem II, which depends on the amount of light the plant receives (Ogawa *et al*., 2004). It is also possible that some protein associated with blooming is activated or deactivated by GSH content, as suggested by Ito *et al*. (2003).

Another explanation is that it may be due to increased FyPP activity (a flowering-specific phytochrome associated protein phosphatase) on the phytochrome kinase. The phytochrome-FyPP interaction is influenced by the light quality and phytochrome phosphorylation status (Kim *et al*., 2002).

Finally, it may also be due to the limitation in the amount of blue light. It has been reported in Arabidopsis that a signal mediated by a cryptochrome (Cry), a blue light photosensor stabilizes CONSTANS (CO) protein, which promotes the transcription of FLOWERING LOCUS (FT). Afterwards, FT protein moves towards the apical meristem to induce flowering. In darkness (short days or shading), COP1, an E3 ligase, degrades CO protein by preventing plant blossoming (Valverde *et al*., 2004; Liu *et al*., 2008). The possible blue light-mediated signal could be a cry-CIF (cryptochrome interacting protein) similar to what happened with the phytochrome-PFI interaction.

Conclusion

The development and flowering (time and quantity) of *J. curcas* was inversely dependent on the amount of light received.

Acknowledgements

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