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Combined effects of low light and water stress on *Jatropha curcas* L. promotes shoot growth and morphological adjustment

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ABSTRACT

Jatropha curcas (physic nut) is a plant with economic and pharmaceutical uses. Basic studies on the influence of environmental factors on the early development of *J. curcas* are important for improving farming techniques and increasing productivity. This study investigated the adjustments of *J. curcas* to the environmental factors of drought and light stress in order to determine which factors most strongly affect the allocation of biomass during early growth. Leaves, stems, and roots of young plants were sampled and leaf area was measured during January and June in 2011. Plants of *J. curcas* that were grown in shade and subjected to water stress showed higher biomass allocation to aerial parts (mainly stems), which can be explained as a strategy for maximizing carbon assimilation. The pattern of biomass allocation between aerial components and the root system changed in plants grown in shade. During June 2011, biomass in shade-grown *J. curcas* was preferentially allocated to stems, indicating long-term adjustment. The lower biomass allocation to the root system suggests reduced exploitation of soil water even when this resource is scarce. Thus, over the long term, growth of *J. curcas* may be compromised by the combined effects of light stress and water deficit.

Keywords: growth, *Jatropha curcas*, leaf area, light stress, water deficit

Introduction

The physic nut (*Jatropha curcas*, Euphorbiaceae) is a multipurpose plant with economic and pharmaceutical potential. One of the most important economic use is the production of oil extracted from seeds (Gübitz *et al.* 1999; Augustus *et al.* 2002; Tiwari *et al.* 2007), which is used for biodiesel production. *Jatropha curcas* can be used as hedge plantations since it does not serve as food for cattle, additionally can be used to control soil erosion (Heller 1996), and its oil can be used to produce soap and lamp fuel (Gübtiz *et al.* 1999). The pharmaceutical uses are performed using the plant latex as healing, hemostatic and as a purgative (Peixoto 1973). A small tree (up to 5 meters tall), *J. curcas* grows in a wide range of water regimes (200–1500mm) and drops its leaves when subjected to long periods of drought. However, net primary productivity of physic nut increases during periods of increased rainfall. The species is widespread because of its traits and its capacity to tolerate drought, low radiation, and low soil fertility, and its adaptability to highly variable climatic conditions (Putten *et al.* 2010).

In plants, stress can occur when there is a deviation from the optimal conditions for growth and development, and if the plant's thresholds for resistance and adaptability are exceeded, permanent damage or death can result. Leaf water potential and plant physiological processes including stomatal resistance, transpiration, and photosynthesis can be influenced by short-term water stress (Chapin III *et al.* 1987), and acclimation to different light intensities can manifest physiologically and morphologically (Chazdon *et al.* 1996). Shading results in reduced photosynthesis because shaded leaves are light limited and thus contribute little to overall productivity, unlike leaves exposed to full sunlight. Sun leaves have less surface area and greater weight per unit surface area than shade leaves (Almeida *et al.* 2005). Besides, shaded leaves show low leaf thickness, stomatal density, leaf area index than sun leaves and its leaves had horizontal orientation (Givnish 1988) than sun leaves. Shade plants can be more affected by seasonal water deficit than sun plants in function of competition of nutrients by roots and low photochemical efficiency (Valadares & Pearcy 2002). Young plants under dry forest canopy (Khurana & Singh 2001) and in Cerrado vegetation (Ronquim *et al.* 2009) develop adaptive traits such as high biomass allocation to the roots. In this way, these plants under light limitation and soil water stress allocate resources to produce new biomass to the organs that acquire the most strongly limiting resources (Chapin III *et al.* 1987).

Jatropha curcas plants grown in light-limited environments are taller than those grown in full sun (Costa *et al.*

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2011). Deep shading can decrease photosynthetic performance and thus biomass production in *J. curcas* (Matos *et al.* 2011), but moderate shade improves temperature and humidity conditions for plant growth and can increase production of total dry mass, leaf dry mass, and leaf area (Matos *et al.* 2011). *Jatropha curcas* grown in full sun showed higher net carbon assimilation rate, quantum yield, and dissipation of excess light energy than shaded individuals (Matos *et al.* 2009).

Under stress, plants show long-term changes that are reflected in leaf area and biomass allocation between different crown tissues (leaves and shoots). The pattern of biomass allocation between leaves and shoots also indicate how a species optimizes resource use and determines crown architecture (Souza *et al.* 2009). *Jatropha curcas* shows significantly non-uniform growth, development, and crown architecture because this species has not been bred for genetic improvement (Albuquerque *et al.* 2009). Thus, basic studies of the morphology of *J. curcas* are necessary to obtain a better understanding of its growth and acclimation processes, which will help in the genetic improvement of this species. Experiments that examine factors such as water deficit and light stress are also important in the context of global climate change and uneven patterns of precipitation and temperature (Melillo *et al.* 1993; Vitousek 1994; Hughes 2000), such as increased atmospheric vapor pressure deficit.

In this study, we assessed the long-term response of *J. curcas* plants subjected to water and light stresses by determining biomass allocation among leaves, stems, and roots. Our hypothesis is that individuals of *J. curcas* plants growing in shade will present higher height, leaf area, specific leaf area and leaf area ratio in comparison with individuals growing under high light intensity. However, because of possible synergism between light and water stresses along experiment, individuals under these stresses could decrease production and biomass allocation to stem, roots and leaves. We expected that shade environment could improve the microclimatic conditions to growth of *J. curcas* plants, but when subjected to long term water stress the shade environment will become a high stressor and will impaired *J. curcas* development. Our findings may help in the management of *J. curcas* by improving the performance of plantings to increase their productivity.

Material and Methods

Plant material, experimental and soil conditions

Jatropha curcas L. develops as a shrub or small tree and has a lifespan of approximately 50 years. The crown architecture varies from a main stem with no branches to a main stem with branches growing from the base. Branches of *J. curcas* contain sticky, white latex, and the root system is well developed, with roots growing laterally and vertically into deeper soil layers. This species is resilient and can survive in temperatures from 4° to 35.7°C, annual precipitation from 440mm to 3121mm and in locations with short growing seasons. It can retrieves nutrients from its leaves and store them in the stem and root system (Putten *et al.* 2010). The leaf habit is deciduous, but the stem remains green and photosynthetically active after the plant drops its leaves (Putten *et al.* 2010).

Seeds of *J. curcas* used in this study were collected in the city of Janaúba, Minas Gerais, Brazil, and were stored for 5 months in plastic bags in the laboratory at 25°C. The seeds were sterilized with a solution of 2% sodium hypochlorite (NaOCl) for 2 min and then were washed with distilled water. The sterilized seeds were placed on germination paper moistened with deionized water and were maintained in a germination chamber (28°C, 100% relative humidity, 12-h photoperiod) for 9 days. After germination, healthy seedlings were selected according to morphological homogeneity and were transferred to plastic pots containing 8 L of soil. The soil used in the experiment was classified as mesotrophic. The soil chemical characteristics at the beginning of the experiment were: 26 g dm^{-3} of total organic matter, pH value 5.25 under water, cation exchange capacity 7.13 $cmol_c\,dm^{-3}$ and saturation base (V%) equal to 34.1, 2.20 and 135 mg dm^{-3} of phosphorus and potassium, respectively, and 1.53 and 0.55 $cmol_c\,dm^{-3}$ of calcium, and magnesium, respectively.

The experiment was performed in a greenhouse with four treatments designed to assess the interactions between light stress and drought. Ten plants were maintained under full sunlight with daily watering (Sun + daily watering, DW); 10 plants were kept under full sunlight with cyclical suspension of watering (Sun + water stress, WS); 10 plants were grown under 70% shade tissue with daily watering (Shade, light stress + DW); and 10 plants were covered with 70% shade tissue with cyclical suspension of watering (Shade, light stress + WS). In the water-stress treatments, plants were kept without irrigation until signs of stress were evident (e.g., leaf tipping and wilting), after which the plants were irrigated to soil field capacity. Thus, we investigated the individual and synergistic effects of the stresses. Sampling was performed in 2011 at 210 days after sowing (DAS, January) and 360 DAS, in June.

Biometry, leaf area, shoot and leaf dry mass

We recorded weekly the plant height and petiole length in five plants per treatment using a millimeter ruler, and we measured the diameter of the stem base (approximately 2cm from ground level) using a vernier caliper. The number of leaves was also recorded weekly. These traits were measured from October 2010 to June 2011.

Another group of five plants per treatment was used for destructive measurements of stem, root, and leaf dry weight and leaf area. Stem dry weight was determined after removing all lateral buds and leaves, and the area and weight of the removed leaves was determined. Leaf area was determined using Image Pro version 4.0 (Media Cybernetics, Rockville, MD). Stems, roots, and leaves were dried out at 70°C to constant weight (Cornelissen *et al.* 2003) and their masses were measured with a precision balance. Before drying, the length of stems and roots was measured with a millimeter ruler. All leaves were assessed, regardless of size and age. The leaf area per stem (individual) was obtained from the sum of the leaf areas for that stem, and total leaf area and the mass of stems, roots, and leaves were determined on a per-plant basis.

Shoot–foliage relationships

The following biometric indices were calculated from the measured morphological characteristics: specific leaf area (leaf area / leaf mass; cm^2 g^{-1}); weight-based root-to-stem ratio (root dry mass / stem dry mass; g); length-based root-to-stem ratio (root length / stem length; cm), leaf area ratio (LAR; total leaf area / total dry mass; cm^2 g^{-1}) and leaf display index (leaf area per stem length; cm^2 cm^{-1}). These morphological indices show the distribution of foliage in the plant crown and the optimization of biomass allocation among stems, roots, and leaves (Yagi & Kikuzawa 1999; Yagi 2000; Souza *et al.* 2009). The distribution of foliage also indicates how the plant uses available resources and adjusts to stresses such as drought and shade.

Statistical analyses

The experiment followed a factorial (2 × 2) design with two conditions of luminosity (full sun and shade) and two levels of water availability (water stress and well watered). We calculated the mean and standard error for all morphological and biometric indices (n = 5 plants per treatment) and used two-way analysis of variance (ANOVA). The means were compared by Tukey's test at 5% probability with SAEG 9.1-UFV software (Fundação Arthur Bernardes, UFV, Viçosa, 2007). Only when required the data were grouped into sub-divided parcels, with each parcel representing the time of sampling. We do not compare the temporal differences related to leaf parameters among treatments, once plants grown in full sun lost their leaves in June 2011.

Results

Water stress in combination with exposure to shade affected leaf area and stem length during the first data collection (January 2011). The effect of water stress on average leaf area was more severe in plants exposed to full sunlight with reduced dry masses of stem, roots, and leaves (Tab. 1). In June 2011, second data collection, all *J. curcas* plants grown in full sun lost their leaves, and shade-grown plants exposed to water stress had reduced leaf area and leaf dry

Table 1. Morphological traits of physic nut (*Jatropha curcas* L.) subjected to light and water stresses during January and June 2011. ANOVA results are presented in the rows below each season's data. Significance levels are indicated as follows: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$; ns, not significant. Significant differences are indicated by different capital or lower case letters: capital letters compare sun versus shade treatments, and lowercase letters compare well-watered (WW) versus water-stressed (WS) treatments (Tukey's test, α= 0.05). Data are means ± standard error of five replicates.

Morphological traits

January 2011

Treatments		**Average leaf area (cm²)**	**Total leaf area (cm²)**	**Stem dry mass (g)**	**Root dry mass (g)**	**Leaf dry mass (g)**	**Total dry mass (g)**	**Stem length (cm)**	**Root length (cm)**
Sun	**WW**	49.6 ± 5.2Ba	367.3 ± 47.7Ba	2.9 ± 0.4	1.5 ± 0.2	1.3 ± 0.1	5.8 ± 0.7	13.4 ± 0.8Ba	13.0 ± 0.4
	WS	26.9 ± 1.5Bb	203.0 ± 20.4Ba	1.9 ± 0.4	1.0 ± 0.2	0.8 ± 0.1	3.6 ± 0.7	10.3 ± 1.1Ba	11.9 ± 1.0
Shade	**WW**	97.5 ± 2.2Aa	757.9 ± 75.9Aa	3.2 ± 0.5	1.2 ± 0.1	1.5 ± 0.1	6.0 ± 0.5	16.5 ± 1.3Aa	15.0 ± 0.6
	WS	104.4 ± 7.4Aa	922.7 ± 63.5Aa	2.5 ± 0.4	0.9 ± 0.1	1.2 ± 0.1	4.6 ± 0.6	18.5 ± 1.3Aa	12.0 ± 0.5
Light (L)		***	***	ns	ns	*	ns	***	ns
Water (W)		ns	ns	*	**	**	*	ns	*
L × W		**	**	ns	ns	ns	ns	*	ns

June 2011

Treatments		**Average leaf area (cm²)**	**Total leaf area (cm²)**	**Stem dry mass (g)**	**Root dry mass (g)**	**Leaf dry mass (g)**	**Total dry mass (g)**	**Stem length (cm)**	**Root length (cm)**
Sun	**WW**	–	–	4.2 ± 0.9	2.4 ± 0.3Ba	–	6.5 ± 1.3Ba	13.6 ± 1.4	13.4 ± 1.2
	WS	–	–	2.5 ± 0.3	1.6 ± 0.2Bb	–	4.1 ± 0.4Bb	12.8 ± 0.6	13.0 ± 0.9
Shade	**WW**	102.8 ± 5.8	777.5 ± 33.6	21.1 ± 2.2	10.2 ± 1.2Aa	1.7 ± 0.1	33.0 ± 3.3Aa	25.6 ± 1.6	14.1 ± 0.8
	WS	68.8 ± 32.0	137.1 ± 64.3	15.4 ± 1.2	6.0 ± 0.2Ab	0.5 ± 0.1	21.9 ± 1.4Ab	28.4 ± 2.2	15.0 ± 0.6
Light (L)		-	–	***	***	–	***	*	ns
Water (W)		ns	***	**	**	***	**	ns	ns
L × W		-	–	ns	*	–	*	ns	ns

mass relative to plants grown in shade with adequate water supply (Tab. 1). There were no differences in root length among treatments.

High light exposure had significant effects on all biometric indices in the January and June 2011. In January 2011, the highest leaf display index, specific leaf area, and LAR occurred in plants grown in shade (Tab. 2). At this time, significant increases in LAR in water-stressed treatments occurred only in shade-grown plants. In contrast, reduced LAR occurred in shade-grown plants subjected to water stress in June (Tab. 2). The lowest root-to-stem ratio occurred in plants grown in shade during both evaluation periods. The root-to-stem ratio (mass basis) increased in June 2011, but on a length basis, the root-to-stem ratio decreased relative to January. The leaf display index increses in June 2011 and LAR was lower in June than in January 2011 (Tab. 2). Light stress affects petiole length ($P<0,01$, ANOVA), being in shaded plants (12.5 cm) three times higher than in sunny plants (4.3 cm).

Discussion

The higher biomass allocation to stems of *J. curcas* plants grown in shade (June 2011) and the high investment in leaf area in shaded plants indicates that these were morphological adjustments to stress (Tabs. 1, 2). These adjustments enable establishment and growth of *J. curcas* under low light conditions (Ronquim *et al.* 2009; Sesma *et al.* 2009), thus avoiding the effects of light deficit (Bloom *et al.* 1985). Species that develop in shaded environments have strategies for increasing the area of tissues that can absorb light (Givnish 1988; Almeida *et al.* 2005). According to Costa *et al.* (2011) and Sesma *et al.* (2009), *J. curcas* plants subjected to 50% shading showed greater height, leaf area, and total dry mass than plants grown in full sun. These authors suggested that better performance of shaded *J. curcas* could be related to better temperature and humidity conditions in the shade. However biomass allocation can vary as a result of distinct genetic traits leading to different physiological adjustments.

However, when shaded *J. curcas* plants were subjected to long-term cycles of water deficit, biomass allocation to roots was reduced by more than 40% (Tab. 2), but root length did not change under water stress, so access to the soil water was maintained. This effect of water stress on biomass allocation to roots indicates that the combination of shade and drought could impair plant development under long-term exposure to shade. The decreased biomass allocation to roots could also be caused by faulty translocation of photoassimilates from leaves to roots in shaded plants (Lee *et al.* 1997). This indicates that *J. curcas* is adapted to dry conditions; however, this vegetative growth was not associated with production

Table 2. Biometric indices in physic nut plants (*Jatropha curcas* L.) during January and June 2011. ANOVA results are presented in the rows below each season's data. Significance levels are indicated as follows: *, p<0.05; **, p<0.01; ***, p<0.001; ns, not significant. Significant differences are indicated by different capital or lower case letters: capital letters compare sun versus shade treatments, and lower case letters compare well-watered (WW) versus water-stressed (WS) treatments (Tukey's test, α= 0.05). Data are means ± standard error of five replicates.

Biometric indices

January 2011

Treatments		Leaf display index (cm^2 cm^{-1})	Specific leaf area (cm^2 g^{-1})	Root/stem ratio (cm)	Root/stem ratio (g)	Leaf area ratio (cm^2 g^{-1})
Sun	WW	3.7 ± 0.2	40.0 ± 2.9Ba	1.0 ± 0.1Aa	0.5 ± 0.0	63.5 ± 4.0Ba
	WS	2.8 ± 0.4	36.8 ± 4.3Ba	1.2 ± 0.2Aa	0.5 ± 0.1	61.7 ± 9.0Ba
Shade	WW	6.1 ± 0.5	65.2 ± 4.6Aa	0.9 ± 0.1Aa	0.4 ± 0.1	128.5 ± 12.7Ab
	WS	5.8 ± 0.8	88.8 ± 8.3Aa	0.6 ± 0.0Ba	0.3 ± 0.0	208.1 ± 22.8Aa
Light (L)		***	***	*	*	***
Water (W)		ns	ns	ns	ns	*
L × W		ns	*	*	ns	*

June 2011

Treatments		Leaf display index (cm^2/cm^{-1})	Specific leaf area (cm^2 g^{-1})	Root/stem ratio (cm)	Root/stem ratio (g)	Leaf area ratio (cm^2 g^{-1})
Sun	WW	–	–	1.0 ± 0.1	0.7 ± 0.1	-
	WS	–	–	1.0 ± 0.1	0.6 ± 0.1	-
Shade	WW	33.0 ± 3.3	58.8 ± 3.3	0.6 ± 0.1	0.5 ± 0.0	24.7 ± 3.0
	WS	21.9 ± 1.4	150.8 ± 70.2	0.5 ± 0.1	0.4 ± 0.0	5.7 ± 2.6
Light (L)		-	–	***	*	–
Water (W)		ns	ns	ns	ns	**
L × W		-	–	ns	ns	–

(flowers and fruits) because the plants were not mature (Albuquerque *et al.* 2009).

Developmental impairment of *J. curcas* resulting from synergy between stresses was revealed when plants under full sun were subjected to water stress. *Jatropha curcas* plants have reduced leaf area when grown in dry conditions (Albuquerque *et al.* 2009) or under full irradiance (Matos *et al.* 2009). Here, we have shown the combined effects of light stress and water deficit on this species for the first time.

Leaf size was significantly reduced in plants grown under full sun and water stress relative to that of plants grown in shade (Tab. 1). Water stress affects cell turgor, which limits leaf growth and development (Fahn *et al.* 1990). Thus, the lower evaporative demand under shade conditions may have contributed to the maintenance of leaf size under water stress. Changes in biomass allocation in relation to unchanged leaf area in these plants demonstrate a close relationship between the water and carbon balance during periods of water deficit.

Considering the optimal maximum temperature (31.5–34.0°C) in the natural range of *J. curcas* (Maes *et al.* 2009), we suggest that *J. curcas* grown in full sun lost their leaves during June 2011 because of high temperatures (at this time range from 40°C to 50°C). Thus, shaded plants accumulated more biomass in June 2011 (second sampling), which resulted in a positive carbon balance for these plants. This response allows plants grown in shade to minimize the growth-limiting effects of drought. However, during the second evaluation period, the reduction in root dry mass in shade-grown plants was higher (–42%) under water stress than under full sun (–33%), indicating that even under drought, plants grown in shade spend more resources on shoot growth, as demonstrated by the root/stem ratio (cm).

Biomass allocation to foliage in plants in shaded dry environments ensures more chance of light capture for photosynthesis (Ronquim *et al.* 2009). Accordingly, *J. curcas* adapt to low light availability by growing toward the light to maintain photosynthesis. The higher leaf display index and leaf area ratio in January 2011 in shade-grown *J. curcas* indicated resource allocation for optimizing light interception (Yagi & Kikuzawa 1999; Yagi 2000). Matos *et al.* (2009) showed that *J. curcas* grown in shade had higher leaf area and leaf chlorophyll content. Leaf morphophysiological adjustments can generate more surface area for light capture and absorption (high leaf chlorophyll content). Thus, shaded plants increase photosynthetic area by allocating resources to aerial tissues. Increased LAR in response to shading can offset decreased net assimilation (Hoffmann & Franco 2003), as observed in shade-grown plants under water stress during the first measurement period.

During the second sampling period (June 2011), shaded plants had increased leaf display index and decreased LAR relative to the first sampling period (January 2011). The high leaf display index is a result of diminished stem length and continuous leaf production in shaded plants even under water deficit. However, LAR declined in plants subjected to shade and water stress because of decreased leaf area and a shift in biomass allocation to stems. The sampling in June 2011 highlighted the pattern of biomass allocation to stems in plants subjected to shade and water stress. Although *J. curcas* is cultivated under a wide range of water regimes (Maes *et al.* 2009), water deficit, especially during early development, could be decisive in determining plant survival and development.

The greatest mean height occurred in shade-grown plants, reflecting investment in the production of photosynthetic structures to overcome light limitation (Ortega *et al.* 2006). Plants grown in sun do not need to invest heavily in vertical growth for light interception because light is not a scarce resource. The fewest leaves occurred in water-deficit treatments because of senescence of old leaves. Senescence reduces water loss by leaf transpiration, and resources in old leaves can be translocated to young leaves. *Jatropha curcas* can retrieves nutrients from leaves and store them in the stems and roots (Putten *et al.* 2010). Petiole length was greater in shaded than in sun-exposed plants throughout the experiment. *Jatropha curcas* leaves are alternate and sub-opposite and spirally arranged, which enhances the efficiency of light capture (Albuquerque *et al.* 2009). High leaf area per stem in shaded plants causes intense self-shading among leaves and the longer petioles would improve sunlight capture. The phenotypic response to shade of maximizing shoot dry mass and plant height is a typical strategy for adapting to low light conditions. These responses depend on genetic traits and plant-environment interactions (Moraes Neto *et al.* 2000).

The global distribution of *J. curcas* covers a diversity of climatic conditions (Maes *et al.* 2009), but it is predominately found in tropical savannas and tropical monsoon climates. According to Maes *et al.* (2009), *J. curcas* is common in regions where rainfall exceeds 944 mm year^{-1}. Experiments examining light conditions show that *J. curcas* grown in sunny areas develop better than those grown in shade (Matos *et al.* 2009; 2011). However, *J. curcas* cannot be classified as an obligatory heliophyte because plants grown in 50% shade perform better than those grown in full sun (Costa *et al.* 2011). Thus, *J. curcas* can withstand low light regimes or moderate water stress, but the co-occurrence of these stresses, as investigated here, can result in decreased development.

Conclusion

Under the combined stress of water deficit and low light, patterns of biomass allocation in *J. curcas* are altered in favor of stems to offset a potential decrease in carbon assimilation. Productivity is linked to photosynthetic capacity, and biomass allocation is related to plant development. Thus, under water stress, *J. curcas* plants grew better in shade than in full sun. However, plant development may be impaired by long-term shade and drought because of synergistic effects between these stresses.

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