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Hydraulic conductivity in stem of young plants of *Jatropha curcas* L. cultivated under irrigated or water deficit conditions

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A B S T R A C T

Jatropha curcas L. can survive situations of water deficiency, in which carbon assimilation and growth rates are severely affected, which can ultimately result in low productivity. With the objective of evaluating the hydraulic conductivity of stem xylem and its relationship with leaf gas exchange under water deficiency, two-month old plants of ten genotypes of *J. curcas* from an improved population were cultivated under water restriction (soil water content of 14%) or under full irrigation (soil water content of 22%) for 60 days. Water deficit led to significant increase of leaf area-specific hydraulic conductivity (LSCn) in genotype CNPAE 517 and decrease in CNPAE 556, 557, 559, 569 and 570. Of those five genotypes, only in CNPAE 556 there was no decrease of leaf water potential measured around 4 h. Genotypes CNPAE 516, 517 and 520 can be highlighted, where elevated rate of net photosynthesis were observed even under water restriction. Changes in the anatomy of the xylem vessels, as well as in root biomass when submitted to water deficiency favored a greater or lesser drought tolerance of the genotypes when the native or potential hydraulic conductivity were analyzed. In summary, high plasticity for hydraulic and anatomical traits, as observed for the genotypes CNPAE 516, 517 and 520 must be considered for further investigation on the tradeoffs between hydraulic conductivity and productivity, in the search for genetic material suitable for cultivation in areas subject to short periods of soil water deficit.

1. Introduction

The process of manufacturing biodiesel from vegetable oil tends to increase the water demand, which may render the production of certain species unviable for this purpose. Therefore, modern agricultural practices should incorporate increased efficiency in the use of water through genetic improvement for drought tolerance, in addition to localized irrigation technologies and economical water supply. In this context, *Jatropha curcas* L. is an oilseed species of the Euphorbiaceae family, considered a very promising oleaginous for biodiesel production (Sato et al., 2007; Carneiro et al., 2009). Traits indicative of tolerance to water deficiency have been identified, although certain studies have reported negative responses to water deficit, despite its survival and good recovery capacity (Fini et al., 2013; Sapeta et al., 2013; de Santana et al., 2015; de Oliveira et al., 2016). According to Wani et al. (2016), current genotypes still present low productivity (500–1000 kg ha^{-1}) and although this crop has been quoted as drought tolerant, it requires high water availability (750–1000 mm) in order to reach economically viable production.

Plant productivity is directly related to the carbon fixation capacity, which makes the study of the causes of photosynthetic changes a significant element in the search for increased yield for the species. Water stress studies in *J. curcas* have demonstrated that its relative drought tolerance is related to stomatal control of transpiration, despite the effects of water stress on growth and the process of absorption of water and minerals by the roots (Sapeta et al., 2013; Fini et al., 2013; Yin et al., 2012). Knowledge on long-distance transport processes in plants is important as, among others, it may help to explain the distribution of species on the planet (Gleason et al., 2015). This transport is considerably relevant for the replacement of water lost by the transpiration process, in the prevention of dehydration and for the consequent maintenance of the photosynthetic system. In angiosperms, this

Abbreviations: A, net photosynthesis; *A/gs*, intrinsic water use efficiency; DAIT, days after initiating treatment; *E*, transpiration rate; *gs*, stomatal conductance to water vapor; K_{max}, maximum hydraulic conductivity; K_n, native hydraulic conductivity; Kp, potential hydraulic conductivity; K_s, hydraulic conductivity in stem segments; LDM, leaf dry mass; LSC, Leaf area-specific hydraulic conductivity in stem segments; PAR, photosynthetically active radiation; PLC, percentage of loss of conductance; RWC, relative water content; SWC, soil water content

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transport is carried out in the vessels elements of the xylem, conferring advantages and disadvantages for acclimatization of plants to different water conditions, and favoring the survival and reproduction (Tyree and Ewers, 1991). In light of this, studies on the plant's hydraulic architecture can provide data on the plant's ability to meet the water requirement of both photosynthetic and growth tissues (Melcher et al., 2012).

The most common plant responses to limited water availability is to reduce transpiration rate by stomatal closure or to drop the leaves aiming to decrease water loss through evaporation during the dry season. However, there has been decrease of hydraulic conductivity (K_L) in the aerial part of plants growing under limited water availability, probably due to the reduction in the number or size of the xylem vessels, which plays a central role in the hydraulic architecture of the plant as it can influence conductivity (Nijsse et al., 2001), growth potential (Solari et al., 2006), as well as the capacity to deal with drought (Zimmermann, 1983). Hydraulic properties of xylem play an essential role in supporting growth and photosynthesis, influencing the sensitivity to environmental conditions such as drought and frost, stem hydraulic conductivity can be used as a comparative measure of hydraulic adaptation by species, as well as to assess the impact of environmental variation, especially drought, on water transport (Melcher et al., 2012).

Several methods are used to measure hydraulic conductivity of the xylem (Sperry et al., 1988; Melcher et al., 2012). The flow of water through the xylem vessels, considering them to be fully tubular, results in a ratio between the volumetric flow rate and the applied pressure gradient, which is proportional to the 4th power of the vessel radius, as given by the Hagen-Poiseuille equation (Lewis and Boose, 1995; Zwieniecki et al., 2001; Melcher et al., 2012). However, since the anatomy of the xylem vessels is not as simple as in artificial hydraulic systems, the xylem hydraulic conductivity values calculated from this method overestimate the hydraulic conductivity by about five times the measured value (Lovisolo and Schubert, 1998), because it does not consider irregularities in vessel structure or the presence of embolism (Tyree and Sperry, 1989).

Embolism is one of the causes of the overestimation of the hydraulic conductivity of the xylem obtained by the method based on the Hagen-Poiseuille equation. Embolism blocks the circulation of the xylem sap and decreases the hydraulic conductivity of the stem. Xylem embolism correlates with plant resistance to drought and growth performance. The reference method for measuring hydraulic conductivity was introduced by Sperry et al. (1988), which consists in estimating the hydraulic conductivity of small stem segments by re-saturating these samples by successive perfusions under low pressure with degassed water. The difference between the initial conductivity and the maximum conductivity reflects the percentage of embolism in the tissue (Bronkhorst, 2008). This technique is used to investigate the occurrence of embolism in several species and to uncover the relationship between embolism, xylem water potential and xylem anatomy (Sperry et al., 1988).

In light of the above, and considering that hydraulic conductivity of the xylem can vary both among genotypes and across growth environments (Melcher et al., 2012), the objectives of this study were (1) to investigate the effects of water deficiency on the hydraulic conductivity of the stem and on the leaf gas exchange in young individuals of *J. curcas*; and (2) to determine if there is genotypic variation for the studied characteristics, considering an improved population of the species. The main hypothesis is that the effects of water stress alter the anatomy of xylem vessels with direct impact on hydraulic conductivity of the stem of *J. curcas* on a genotype dependent way.

2. Materials and methods

2.1. Plant material and experimental conditions

The experiment was carried out between 15 September 2016 and 29 January 2017 (136 days) under greenhouse conditions, at the campus of the State University of Santa Cruz (UESC), located near the urban area of Ilhéus, BA (14°47′00″S, 39°02′00″W).

Table 1
Genotypes of an improved population of *Jatropha curcas* L. and the respective parents from EMBRAPA-Agroenergy, Brasilia, DF, Brazil.

Genotype	Male	Female
CNPAE 516	DIAL-28-5	DIAL-28-6
CNPAE 517	TP-811-1-5	DIAL-3
CNPAE 520	BAG-191-1-5	DIAL-10
CNPAE 528	JATROPT-4	DIAL-16
CNPAE 556	JATROPT-6	BAG-171
CNPAE 557	BAG-144-1-1	BAG-156-1-5
CNPAE 559	BAG-241-2-4	DIAL-7
CNPAE 564	DIAL-7	DIAL-16
CNPAE 569	BAG-167-2-5	JATROPT-10
CNPAE 570	BAG-199-2-5	DIAL-3

Seeds from ten genotypes of *J. curcas*, namely CNPAE 516, CNPAE 517, CNPAE 520, CNPAE 528, CNPAE 556, CNPAE 557, CNPAE 559, CNPAE 564, CNPAE 569, and CNPAE 570, obtained from the crosses described in Table 1, were donated by the EMBRAPA, Agroenergy Centre, Brasília, DF, Brazil. The seeds were germinated in 20 L pots, containing 12 kg of a sandy grade soil. After 40 days of germination, thinning (leaving one plant per pot), and pruning of the apical core were performed so that the production of lateral branches was stimulated. The pots of all treatments were covered with aluminum foil in order to reduce water loss by evaporation and allow for a gradual increase of water deficit.

Watering treatments were initiated 74 days after germination. A set of plants was submitted to a regulated irrigation treatment, seeking to maintain soil water content (SWC) around 60% of field capacity (SWC = 14%). Remaining plants were maintained under full irrigation, i.e., maintaining SWC around field capacity (SWC = 22%). A Wet sensor (Delta-T Devices Ltd., Cambridge, UK), previously calibrated to the type of soil of the experiment, was used to monitor SWC during the experiment. The values obtained with the WET sensor were used for the calculation of the quantity of water to be reposed in each treatment, which were, on average, around 300 and 500 mL daily, on water deficit and irrigated (control) plants, respectively.

The photosynthetically active radiation (PAR, quantum sensors S-LIA-M003), temperature and relative air humidity (combined sensor S-THB-M008) were monitored during the entire duration of the experiment and the data were automatically stored using an automatic datalogger H21- 002 (Onset Computer Corporation, USA) (Table 2).

2.2. Leaf gas exchange

Leaf gas exchange, as well as all evaluations were performed 60 days after initiating treatment (DAIT), so that all data could be compared with the hydraulic conductivity measurements of the stem xylem, which were completely destructive. Net photosynthetic rate, transpiration rate, stomatal conductance to water vapor and the internal CO_2 concentration were measured between 7 and 12 h in

Table 2
Air temperature (Tair[a]), relative humidity (RH[b]) and total daily photosynthetically active radiation (PAR[c]) over the experimental period.

	Average	Maximum	Minimum
T_{air}	29.1	32.1	25.4
RH	81.9	95.7	70.0
PAR	22.0	26.5	13.7

[a] °C.
[b] %.
[c] mol photons m^2 day 1.