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Research paper

Jatropha curcas L. (Euphorbiaceae) modulates stomatal traits in response to leaf-to-air vapor pressure deficit

Bety S. Hsie [a], Keila R. Mendes [a], Werner C. Antunes [b], Laurício Endres [c], Mariana L.O. Campos [a], Felipe C. Souza [c], Nivea D. Santos [a], Bajrang Singh [d], Emília C.P. Arruda [e], Marcelo F. Pompelli [a, *]

[a] Plant Ecophysiology Laboratory, Federal University of Pernambuco, Department of Botany, CCB, Recife, PE, 50670901, Brazil
[b] Department of Biology, University of Maringá, Maringá, PR, Brazil
[c] Plant Physiology Laboratory, Federal University of Alagoas, Center of Agronomy, Maceió, AL, Brazil
[d] National Botanical Research Institute, Rana Pratag Marg, Lucknow, India
[e] Plant Anatomy Laboratory, Federal University of Pernambuco, Department of Botany, Recife, PE, Brazil

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A B S T R A C T

Cultivation of *Jatropha curcas* in arid and semiarid non-cultivated areas could be a sustainable strategy for stimulating biofuel production without competing with food crops for land and water resources. *J. curcas* is considered a drought-tolerant species; however, the mechanisms that provide tolerance are unknown. Few efforts have been made to understand the connections between stomatal development and environment conditions. Here, we compared changes in stomatal density (SD) and stomatal index (SI) and their influence on gas exchange in *J. curcas*. Plants were cultivated in both rainy and dry regions. We describe a distinctive distribution of stomata under the adaxial and abaxial leaf epidermises, where higher SD may have caused the increase in stomatal conductance (g_s) with positive effects on net photosynthetic rate (P_N). However, when rain was excluded, the variation in g_s was strongly related to vapour pressures deficit (VPD), and VPD was strongly related to the P_N. Thus, our results suggest that *J. curcas* may also contribute mitigating the effect of CO_2 deposition in the atmosphere, given that a remarkable change in SD and other leaf traits was observed in response to seasonal variations. Moreover, multivariate analysis highlights the high sensitivity of *J. curcas* plants to VPD which in turn induces rapid stomatal closure and consequent reduction of P_N for long periods of time which reflect into a change in the pattern of development resulting in higher SI. These results can help us to understand the relationship between stomatal features and gas exchange in response to environment changes.

1. Introduction

Jatropha curcas L., purging nut or physic nut, is a large perennial plant in the Euphorbiaceae family. The species is a large deciduous shrub or small tree, with a life expectancy of up to 50 years [1]. In recent decades, *J. curcas* has become popular because of its properties and uses. *J. curcas* seeds contain approximately 25–58% oil [2,3], that can be extracted and converted to biodiesel. The oil can also be used as cooking or lighting fuel, medicine, a biopesticide, and for soap making. Oil extraction by-products can be used as organic fertilizer, combustible fuel, or for biogas production [4]. Production of *J. curcas* as an energy crop has been proposed as a sustainable use of non-cultivated and marginal areas in arid and semiarid regions [5,6] characterized by high evaporative demand and low water availability [7]. Although all recent studies confirm the high drought resistance of *J. curcas* [8–10], there is a lack of information on leaf traits particularly on the effect of seasonal changes in leaf water potential on stomatal functioning and photosynthesis characteristics.

The ability of species to respond to a new environments is critical for growth and survivals [11]. Leaf structures reflect the effects of water deficit more clearly than stems or roots [12].

Abbreviations: CCA, canonical correlation analysis; C_i:C_a, ratio of the internal-to-ambient CO_2 concentration; g_s, stomatal conductance; LA, leaf area; OD, ordinary cell density; P_N, net photosynthetic; RH, relative humidity rate; SD, stomatal density; SI, stomatal index; VPD, leaf-to-air vapor pressure deficit; WUE, water use efficiency; WUE_i, intrinsic water-use efficiency.

* Corresponding author.
E-mail address: mfpompelli@gmail.com (M.F. Pompelli).

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Stomatal responses are essential for the acclimation of plants to new environmental conditions and are thus important determinants of plant survival [13,14]. Generally, adaptation of plants to drought requires transitory and long-term mechanisms for maintaining high water potential by increasing water absorption and reducing transpiration [15]. Excessive water loss by transpiration as a result of a high VPD may induce stomatal closure. However, gas exchange in higher plants is mainly determined by both stomatal opening (pore aperture) and stomatal anatomical features (size and density) [16]. Consequently, the effect of environmental features on leaf conductance involves both long-term processes and short-term dynamics. Short-term events are mediated by adjustments in pore aperture and are reversible, while long-term processes refer to leaf expansion and involve stomatal size and density [17,18]. Aasamaa and Sõber [19] compared the effects of different environmental conditions and found that the stomata of six temperate deciduous tree species grown in a greenhouse responded more strongly to changes in hydraulic environmental factors, *e.g.*, air humidity and water supply than to changes in photosynthetic environmental factors, *e.g.*, light intensity and air CO_2 concentration. Moreover, in field conditions, several environmental factors converge to change stomatal morphology and physiology [13]. Stomatal diffusion resistance, and hence conductance, is somehow directly related to the size and spacing of stomata on the leaf surface, *i.e.*, a trade-off exists between the size and number of stomata [20].

Most studies of stomatal morphology have focused on the closure mechanism because it is involved in water loss, particularly when plants are grown in high relative humidity (RH) [21]. Other anatomical features involved in water loss have received meager attention. For instance, a negative correlation between stomatal size and stomatal functioning has been described in some species [14,22–24]. However, at the leaf level, g_s is not solely determined by stomatal pore aperture but also depends on stomatal density (SD), pore length and pore depth [21]. Variation in stomatal size will therefore largely determine optimization of water flux under water-limiting conditions [17].

Photosynthesis is particularly sensitive to water deficits, because stomatal closure restricts CO_2 influx and reduces carbon gain as soil water status decreases [8,25]. Understanding how crops in arid and semiarid regions respond to changes in leaf-to-air VPD is important because some climate models predict an increase in temperature and a decline in rainfall in coming decades [26,27], which may affect plant functioning. The objectives of this study were therefore to determine the response patterns of SD and stomatal index (SI) to different degrees of water restriction and to determine the relationship with gas exchange of *J. curcas* grown in semiarid and semi-humid ecosystems. Thus, we aimed to clarify two questions: (*i*) Does variation in seasonality affect leaf and stomatal traits and carbon gain in saplings of *J. curcas* in semiarid and semi-humid ecosystems? (*ii*) Does the increase in the number of stomata per unit area (*i.e.*, SD) affect gas exchange of this species?

2. Material and methods

2.1. Study site and plant material

The climate of the state of Alagoas is influenced by weather systems of the intertropical convergence zone and the easterly waves [28], causing highly variable rainfall across the state. The Caatinga ecosystems covers 52% of Alagoas; and is an arid-to-semiarid ecosystem that occupies the region between the Amazon forest and the Atlantic rainforest, covering 735,000 km^2 of northeast Brazil where lives around 28 millions of people [29,30]. This ecosystem includes rainy climates near the Atlantic rainforest and desert-like arid climates in the Caatinga [31]. Regions near the Atlantic rainforest receive more than 4000 mm year^{-1}. In contrast, the Caatinga has high rates of potential evapotranspiration (1500–2000 mm annually) and low rainfall (300–1000 mm annually) that is usually concentrated over 3–5 months [32].

This study was conducted on 5-year old *J. curcas* plants, grown in experimental fields in a semi-humid region near the city of Rio Largo (09°28′42″S, 35°51′21″W, 39 m a.s.l.) and in a semiarid region near the city of Igaci (09°32′13″S, 36°38′01″W, 240 m a.s.l.) (see Ref. [2] for detailed sites description). Compared with Igaci, Rio Largo receives more precipitation annually, has a shorter, less severe dry season and has higher monthly precipitation in both seasons (Fig. 1A). Annual precipitation during the study year (2007) was within the range of historical means of 1700–1900 mm year^{-1} for Rio Largo and 800–1000 mm year^{-1} for Igaci [33]. In both areas, the rains were concentrated mainly in the autumn and winter months from March to August. In both ecosystems, water deficit is caused by soil water deficits and high atmospheric VPD [2,34].

2.2. Stomatal characteristics and leaf area

To ensure that the leaves used in this study had grown during this experiment, all leaves used for morphological evaluations were marked from the primordial stage to full expansion (when sampled). Within each population described above, a fourth

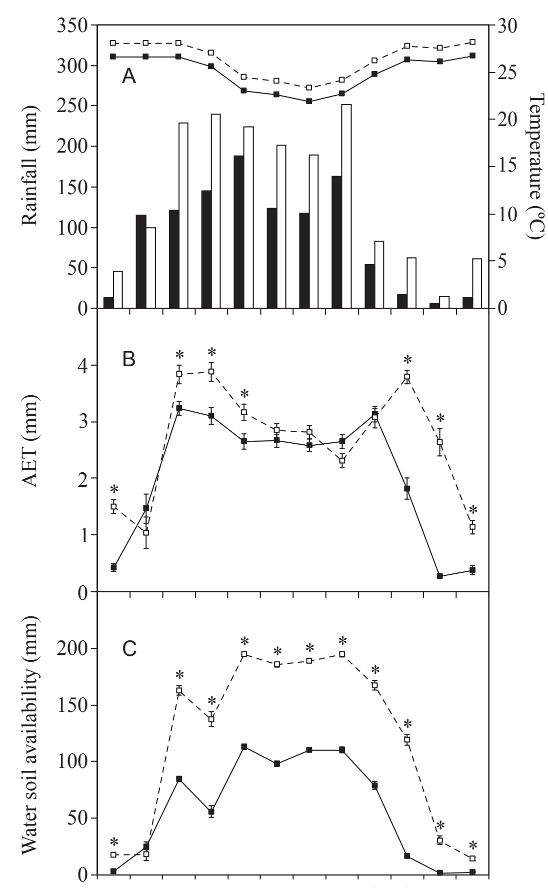

Fig. 1. Climatic characteristics: (A) total monthly rainfall (bars) and mean temperatures (lines); (B) actual evapotranspiration rate (AET) and (C) soil water balance (store) from January to December 2007 in the tropical dry (black symbols) and tropical semi-humid (white symbols) ecosystems. Means followed by asterisks represent statistically significant differences within each month. The values represent the media (±SE), n = 30. Source: Agritempo [79].