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Original Article

Physiological responses of *Cnidoscolus quercifolius* Pohl in semi-arid conditions

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Abstract
This study aimed to evaluate the physiological behavior of faveleira (*Cnidoscolus quercifolius* Pohl) plants grown in the field, in Caatinga, during wet and dry seasons. Adult plants were selected for evaluation in March and April (wet season) and May and June (dry season), during 2016. We evaluated the soil water content, water potential (Ψw), osmotic potential (Ψπ), relative water content (RWC), stomatal conductance (g_s), transpiration rate (*E*), photosynthetic rate (*A*), intercellular CO_2 concentration (*Ci*), instantaneous water use efficiency (*A/E*) and carboxylation efficiency (*A/Ci*). The reduction in water availability in the soil promoted a marked decrease in soil water potential, which was more affected than the relative water content. The opening of the stomata was affected by the decrease in soil moisture content, reducing the stomatal conductance, transpiration rate, photosynthesis rate, instantaneous water use efficiency and carboxylation efficiency. The photosynthesis was more affected than transpiration by the reduction in soil moisture content.
Keywords: Drought tolerance, Caatinga, Stomatal behavior

Introduction

Water availability is the main factor limiting plant growth and survival in semi-arid region of Brazil. The water deficit, combined with the intensive use of soil and disorderly exploitation of forest resources has led to an advanced soil degradation and desertification, because these factors cause changes in water balance patterns. Semi-arid regions are characterized by high temperatures and evaporation rates, with precipitation distributed usually between four and six months during the year. There is an annual variation in rainfall, with periodic droughts occurring in three to five years, with rainfall less than half the annual average, who is around 700 mm (Veloso et al. 2002; Sampaio 2010). The main vegetation component of the semi-arid is the Caatinga, that occurs only in Brazil, which covers 844,453 km^2, corresponding to 9.92% of Brazilian territory (IBGE 2010).

Added to these climatic factors, the soils of the semi-arid region are generally shallow and stony, with low capacity of water retention, making adverse conditions for survival of the vegetal species (Alves et al. 2009). In spite of these factors, the Caatinga has a diversity of environments, with generally deciduous, xerophytic and sometimes prickly vegetation (Veloso et al. 2002). These plants, subject to these environmental conditions that few would support, developed different survival strategies, enabling them to compete for scarce water resources (Dombroski et al. 2011). Although it is the richest dry forest in biodiversity of the world (Holzman 2008), is the Brazilian ecosystem less studied and protected.

Water stress affects physiological process, like photosynthesis, transpiration, respiration, transport and accumulation of assimilates, exerting direct effects on plant growth and production (França et al. 2017; Costa et al. 2015; Klippel et al. 2014; Scalon et al. (2011); Sampol et al. 2003). However, the way that plants respond to drought stress is complex, varies with the species and the age of the plant (Costa et al. 2015).

In recent years, more researches have been developed researches to understand the ecophysiological strategies of Caatinga plants under low water availability, especially during its initial development (Silva et al. 2004; Silva et al. 2004). However, there are few studies in the field, and these studies provide more consistent data than those performed in the laboratory, since there is a greater interaction between the environmental conditions and the physiological responses of the plants (Lacheveque et al. 2011; Ryan 2011).

One of the most representative plant species of the caatinga, the faveleira (*Cnidoscolus quercifolius* Pohl.) is an oleaginous, xerophilic, deciduous species (Maia 2004; Lorenzi 1998), with potential of use for several purposes, as in the recovery of degraded areas, biodiesel production, firewood and animal and human feeding, medicine, sawing, and energy (Maia 2004).

There is a scarce knowledge about the physiology of faveleira and data experimental approach would allow the expansion of knowledge about the specie of this biome aiming the development of strategies that allow a better exploration of its potentialities. Thus, this work was developed with the objective of evaluating the physiological behavior of plants of this species grown in the field during the rainy and early dry season.

Material and Methods

The study was undertaken in an area previously submitted to goat and bovine grazing during 30 years and since 2002 is in the process of recovery with native species of the caatinga (*Mimosa tenuiflora* Poiret, catingueira, and *C. quercifolius*), protected from grazing. This area is located in Nupearido Experimental Farm of the Federal University of Campina Grande (UFCG), Patos, Paraiba, Brazil (7º04'54" S; 30º16'12" W). According to Köppen's classification, the climate of the region is characterized as BS'h', semi-arid, with an annual average temperature above 25 °C and an annual rainfall of less than 1,000 mm/year, with irregular rains (INSA 2012). The predominant type soil in the area is Litholic Neosoil.

The experiment was performed in a randomized blocks design (DBC), with subdivided plots (2 x 4), in which the main plot corresponded to the rainy and dry period and the subplots to the evaluated months (March, April, May, and June), with 4 replicates. Evaluations were performed on three leaves per replicate.

The evaluations were carried out on March 23 and April 22 (rainy season), May 23 and June 25 (dry season), 2016. The year 2016 was considered dry (Figure 1), which had been occurring since 2013. Due to the low rainfall registered and the finding of the beginning of foliar abscission in the faveleira plants, the months of May and June were considered as belonging to the dry season.

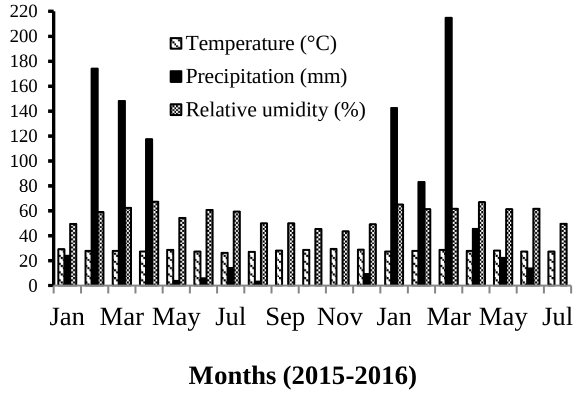

Figure 1. Values of temperature, precipitation, and relative humidity in Patos, Paraiba, Brazil, during January 2015 and July 2016

Net CO_2 assimilation rate (*A*), stomatal conductance (g_s), transpiration rate (*E*), and internal CO_2 concentration (*Ci*) were measured on fully-expanded leaves (three leaves per plant) with an Infra-Red Gas Analyser (IRGA LCpro+ ADC, Hoddesdon, UK). Measurements were performed between 9:00 and 11:00 am, using the atmospheric CO_2 concentration and a photon flux density of 1200 μmol m^{-2} s^{-1}. With the values of *A* and *E*, the intrinsic water use efficiency (*IWUE*) and, with the data of *A* and *Ci*, the carboxylation efficiency (*A/Ci*) was calculated.

After the stomatal evaluations, the leaves were collected, wrapped in aluminum foil and placed in a styrofoam box containing ice, in order to reduce the loss of water to the maximum until they were taken to the laboratory for determination of leaf water potential (Ψw), which was performed using the pressure pump (Scholander et al. 1965), osmotic potential (Ψs) (Bagatta et al. 2008) and relative water content (RWC). This was determined using leaf discs, calculated as $RWC\ (\%) = [(FW-DW)/(TW-DW)]\ X\ 100$ (Dias et al. 2014a), where *FW*, *DW*, and *TW* correspond respectively to fresh weight, weight dry and turgid disc weight. For osmotic potential determination, the leaves were stored in a freezer (-5 °C) for two days. After thawing at room temperature, they were macerated in a mortar, and the extract was subjected to centrifugation (3,000 rpm, for 5 minutes). Then, 2.5 mL of the supernatant was placed in tubes for determination of osmolarity in PZL 1000 Osmometer. The transformation of mosmol kg-1 to MPa was done using the equation $PO\ (MPa) = -c\ (mosmol/kg)\ x\ 2.58\ x\ 10^{-3}$, where *PO* is osmotic potential and *c* is the osmolarity of the sap (Bajji et al. 2001).

At the same time that the above evaluations were performed, soil samples (depth of 0-20 cm) were collected, in a number of four replications, to determine the soil water content by the gravimetric method, according to Embrapa methodology (1997).

All data were analyzed by One-Way Analysis of Variance (*ANOVA*), followed by Tukey´s test for media value comparisons ($P \leq 0,05$), using ASSISTAT software version 7.7 (Silva and Azevedo 2016).

Results and Discussions

Water relations

The highest soil water content was observed in March (10.05%), decreasing in the following months (Figure 2). The rainfall index between January and March 2016 was unsatisfactory, and together with the high temperatures (Figure 1), which favored the high evaporation rates, together with the soil characteristics, SWC can be considered low, possibly due to the soil characteristics (Litholic Neosoil), which is stony and with low moisture retention. In the next months, with decrease rainfall, and the beginning of dry season, soil moisture reached 1.83% in June, representing 82% of reduction, while rainfall dropped from 214.7 mm (March) to 13.7 mm (June) or just 6.4% of the observed value. During the years 2015/2016 the El Niño phenomenon was strong, which has a close relation with the occurrence of drought in the Northeast region of Brazil, particularly in the semi-arid region (Costa 2016).

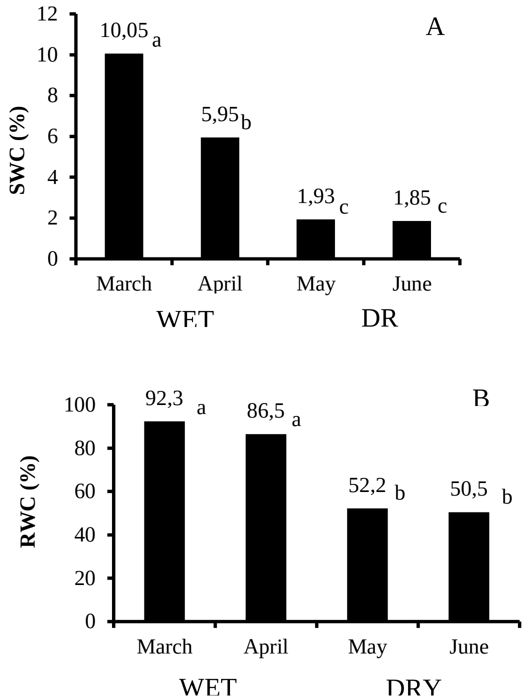

Figure 2. Soil water content (A) and leaves relative water content (B), in the two periods evaluated. Different letters indicated statistical differences between treatments (P ≤ 0.05)

Despite the decrease in soil moisture, from March to April, the RWC of leaves remained high, with no statistical difference between these evaluations (Figure 2B), possible due to the water absorption capacity, maintaining high Ψw (Figure 3). However, as a direct response to the rainfall reduction, and consequently soil moisture, in May and June, there was a strong reduction in tissue hydration, and the RWC reached an average value of 51%, indicating the behavior of faveleira to water availability reduction. According to Pardo (2010), RWC values between 85% and 95% indicate a high state of hydration of the tissues, whereas the value of 50% is considered critical, and can cause tissue death. However, this author adds that some xerophilic species may reach this value and tissue death does not occur.

The direct relationship between the reduction in water availability for plants and the RWC has been verified in several studies, regardless of the methodology used, and the response varies with the studied plant species. Mendes et al. (2013) reported that the leaves water content in *Cordia oncocalyx* maintained in the Caatinga varied from 60% to 70% in the rainy season, falling to 50% in dry season. In *Hevea brasiliensis*, after 35 days without irrigation, Chen et al. (2010) observed a little reduction in the RWC, which was around 70%. Valadares et al. (2014) reported values of 86% in RWC in hybrids of *Eucalyptus grandis* X *E. urophylla*, irrigated every four and six days. These values are higher than those obtained in this research, possibly due to the methodology used since the two studies reported were done in young plants growing in a pot and with controlled irrigation.

As a result of the changes reported in Figure 2, there was a decrease in osmotic potential (Ψπ) and leaf water potential (Ψw) (Figure 3).

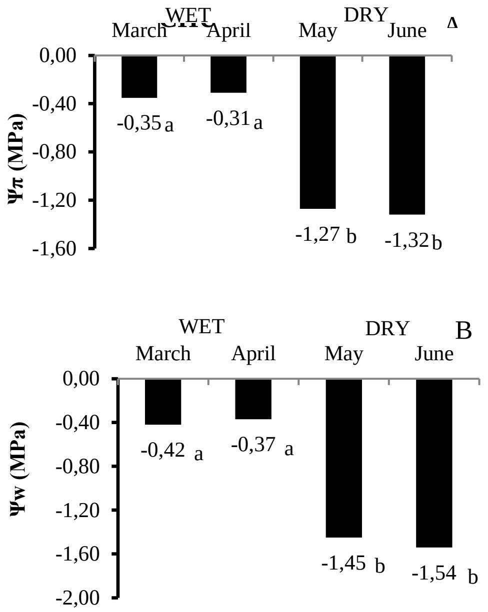

Figura 3. Leaf osmotic (A) and water potential (B) by faveleira, in the two periods evaluated. Different letters indicated statistical differences between treatments ($P \leq 0.05$)

There was no significant differences in Ψπ and Ψw between the March and April, but comparing the wet and dry periods, it is verified that the Ψπ reduced from -0.31 MPa (April) to -1.27 MPa (May) and -1.32 MPa (June) (Figure 3A), representing values about four times lower than those of April. The same was observed in Ψw (Figure 3B), revealing that reduction in water availability for faveleira was accompanied by a strong decrease in Ψπ and Ψw. However, in the above periods, the decrease in the RWC was only 40%, although the value obtained was close to that considered critical (Pardo 2010). The results obtained of Ψw were higher than those found by Dombroski et al. (2011), in *Mimosa caesalpiniifolia*, *Caesalpinia pyramidalis*, *Auxemma oncocalyx*, *Caesalpinia ferrea* and *Calliandra speciosa*.

The highest decrease in Ψπ and Ψw in relation to RWC may have been due to a probable osmotic adjustment (Varone et al. 2012), which is a characteristic of drought tolerant plants (Villar-Salvador et al. 2004). Under water deficit conditions, maintenance of leaf turgor can be achieved by osmotic adjustment (Cordeiro et al. 2009), due to the accumulation of osmotically active compounds such as proline, glycine betaine, sucrose and soluble carbohydrates (Morghaieb et al. 2004).

Gas exchange

In March, due to higher rainfall (Figure 1), were observed higher values of stomatal conductance (g_s), transpiration rate (E), Net CO_2 assimilation rate (A), and lower internal CO_2 concentrations (Ci) (Figure 4).

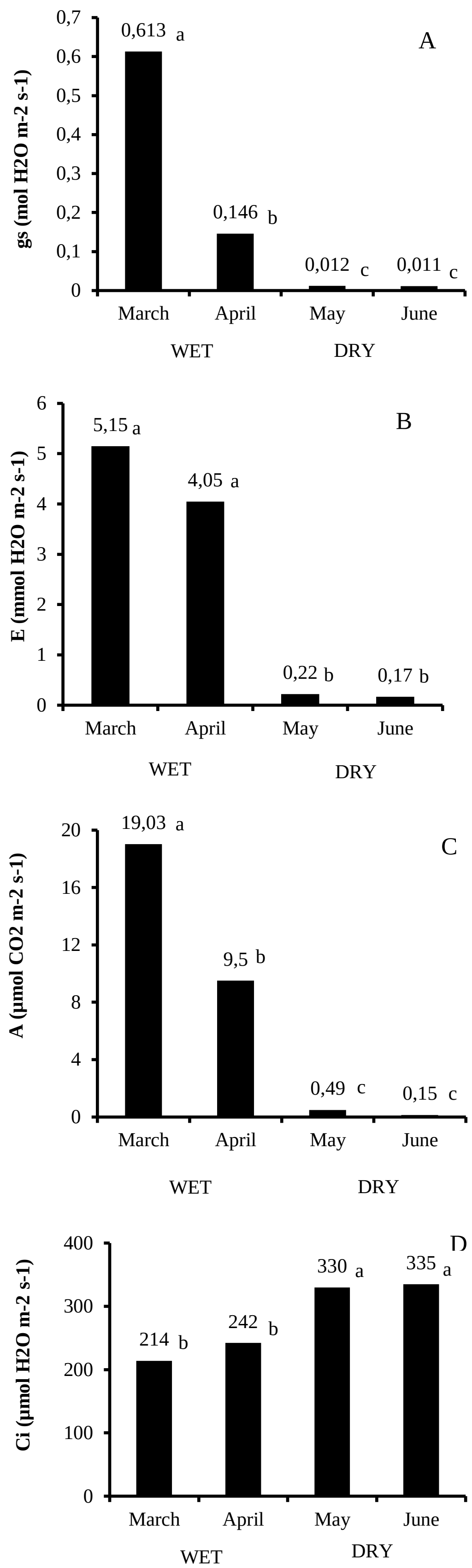

Figure 4. Stomatal conductance (g_s), transpiration rate (E), Net CO_2 assimilation rate (A) and internal CO_2 concentration (Ci) in faveleira, in the two periods evaluated. Different letters indicated statistical differences between treatments ($P \leq 0.05$)

With the soil water availability and SWC reductions occurred stomatal closure, reducing g_s, E e A (Figures 4A, 4B, 4C). It was verified that, in June, the values of *A* corresponded to only 0.8% of those obtained in March (99.2% reduction). In *Ci* there was an increase of 56% (Figure 4D), comparing the rainy season with the dry season.

The SWC reduction (Figure 1A) and in Ψw (Figure 3B) induced a rapid stomatal closure before foliar abscission occurs. With the reduction in water availability, the ABA synthesis and its translocation to stomata, causing its closure (Taiz & Zeiger 2013), minimizing water losses to the atmosphere and conserving the largest amount of water in the soil (Souza et al. al. 2014). This may be advantageous if the drought is prolonged (Sinclair et al. 2005; Martins et al. 2008), situation faced by the faveleira under field conditions. This is one of the first plant species of the Caatinga to initiate foliar abscission with the onset of the dry period, which may be an adaptive strategy to reduce leaf area and, consequently, water loss by transpiration. The abscission is caused by ethylene, accelerating leaf senescence and abscision (Abreu et al., 2015). It can be seen that the above-mentioned changes are strategies quickly employed by the species, aiming to minimize the loss of water. This way, allowing maintenance a good hydration of the tissues, so that the plant can cross the long period of drought and, after the resumption of rainfall, quickly start issuing new leaves.

Due reduction in *A* and increased in *Ci*, there was decrease in *A/Ci* (Figure 4A). This means that although the CO_2 flux (Figure 4D) has not been completely disrupted due to the reduction in g_s, photosynthesis has been compromised. This behavior suggests that biochemical limitations may justify the decrease of *A* (Araújo et al. 2016), leading to reduction in biomass production and growth (Medrano et al. 2002).

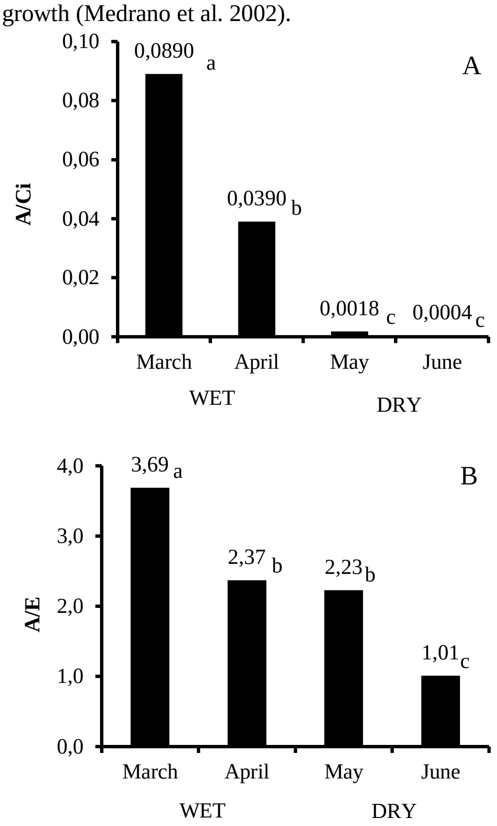

Figura 5. Photosynthetic efficiency (*A/Ci*) and intrinsic water use efficiency (*A/E*) in faveleira, in the two periods evaluated. Different letters indicated statistical differences between treatments ($P \leq 0.05$)

As a result of the effects on the photosynthesis and transpiration rates, there was a decrease in *A/E*, as the soil water content (Figure 2A) and Ψw decreased (Figure 3D). The fact that there is a rapid decrease in leaf water potential and rapid stomatal closure with a reduction in soil moisture, before foliar abscission occurs, indicates the sensibility of the faveleira to the water deficit. According Jones (2004), water use efficiency (WUE) or transpiration efficiency is a conservative characteristic of species and cultivars, and increases with water stress as productivity is reduced. The conservative nature is due to genetic and environmental relationships coupling the plant to its environment (Glen 2010).

According to Taiz and Zeiger (2013), severe water stress causes a decrease in water content of mesophyll cells, affecting photosynthesis and water use efficiency. Rodríguez-Calcerrada et al. (2008) verified lower IWUE in *Quercus pyrenaica* during the dry season. In contrast, Dombroski et al. (2014) found an increase in this parameter in *Handroanthus impetiginosus* plants as the period without irrigation increased, whereas Gonçalves et al. (2009), in *Carapa guianensis*, did not find a significant difference between irrigated and non-irrigated plants. These results reinforce the information that the stomatal responses of the tree species to the reduction of soil water availability vary widely (Gonçalves et al. 2009).

The responses of the stomata seem to be more related to soil moisture content than to the leaf hydration status (Chaves et al. 2009). According to these authors, the stomata respond to chemical signals produced by the roots when the water deficit develops, like abscisic acid (ABA), at the same time that the leaf water status does not change.

The adverse effect of low soil water availability on gas exchange during the dry period has been widely reported. In this sense, Dombroski et al. (2011) reported a reduction in *gs*, *E* and *A* of *Mimosa* caesalpiniifolia, *Caesalpinia pyramidalis*, *Auxemma oncocalyx*, *Caesalpinia ferrea*, *Calliandra speciosa* and *Tabebuia caraiba*, as Ψw decreased. Likewise, in *C. oncocalyx* these physiological parameters were strongly affected by low soil moisture content (Mendes et al. 2013). However, the transpiration was less influenced, similar to that verified in this study. Santos et al. (2013) reported in *Jatropha curcas*, during the dry period, which the higher moisture content of the subsoil forest provided a higher photosynthetic rate than that observed in the Caatinga semi-arid region. In six tree species, Campelo et al. (2015) verified a reduction in gas exchange and the photochemical efficiency of photosystem II in cultivated under irrigated and non-irrigated conditions, during the dry period.

The mechanisms of transpiration control constitute efficient processes to provide or maintain the cellular turgescence under dry conditions (Cordeiro et al. 2009). However, stomatal responses are not influenced only by water availability, since variations in temperature, light, relative humidity and wind speed may also affect them, evidencing the complexity of the stomatal mechanism (Angelocci et al. 2004).

Under controlled conditions, Valadares et al. (2014) reported that the reductions in transpiration and photosynthetic rates were due to stomatal closure, adding that stomatal conductance was more sensitive than those parameters. In *Swietenia macrophylla*, Cordeiro et al. (2009) verified a reduction in gs at the ratio ψw decreasing and verified the close correlation between *gs*, *E*, the total hydraulic conductivity of the plants and the deficit of leaf-air vapor pressure. In plants of *Tabebuia aurea*, it was verified that the values of *E*, *gs* and *A* were null, four days after the suspension of irrigation, demonstrating that the species uses this mechanism to tolerate water deficit since recovery occurred after reirrigation (Oliveira et al. 2011).

The closure of the stomata constitutes one of the first responses of plants to the water deficit, minimizing water losses and, consequently, dehydration of cells and tissues (Albuquerque et al. 2013; Araújo et al. 2016). In addition to promoting the degradation of chlorophyll (Dichio et al. 2005), stomatal closure affects photosynthesis by reducing the availability of CO_2 to ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) enzyme (Pinheiro and Chaves 2011; Dias et al. 2014b), affecting the activity or the capacity and speed of regeneration of the enzyme (Chaves et al. 2009). However, non-stomatal factors may also lead to a decrease in photosynthetic activity under conditions of low water availability (Boussadia et al. 2008). Occurs also losses of the photosynthetic system, as a consequence of the de-structuring of the chloroplast thylakoid membranes (Dias and Brüggermann 2010), decrease in the transport of electrons in the PSII, in ATP synthesis, besides oxidative damage and/or photoinhibition (Galmés et al. 2007).

Conclusions

The faveleira plants maintain elevated water status and gas exchange during rainy season.

Occurs rapid stomatal closure with water availability reduction, reducing transpiration, photosynthesis, photosynthetic efficiency and intrinsic water use efficiency at beginning of the dry season.

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