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Gas Exchange of *Mimosa tenuiflora* (Willd.) Poiret Under Water Deficit and Rewatering

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Abstract

This research aimed to evaluate the physiological responses of *Mimosa tenuiflora* plants submitted to variable water availability conditions during the nursery stage. Twelve-month-old plants kept in plastic pots containing 5 kg of the substrate composed of the subsoil soil mixture and bovine manure (2:1) were submitted to two treatments: irrigated (control) and water stress, which was imposed through the suspension of irrigation, rewatering after seven days of stress. The relative water content (*RWC*) and stomatal parameters were evaluated. The *M. tenuiflora* plants responded quickly to the irrigation suspension, promoting the closure of the stomata, occurring reduction in stomatal conductance, transpiration rate and photosynthesis. The instantaneous efficiency in water use of plants under water deficit remained high only until the middle of the period when irrigation was suspended, and then declined until the last day of the water deficit. After rehydration, the plants showed recovery in all evaluated parameters, indicating that the level of stress imposed did not cause irreversible damages in the cells and tissues.

Keywords: water stress, drought tolerance, water relations

1. Introduction

Mimosa tenuiflora (Willd.) Poiret.), popularly named ‘jurema-preta’, is one of the most commonly woody species in the Brazilian semiarid, belonging to the Mimosaceae family. It is native to the *Caatinga* Biome, but not endemic to the region, and can also be found in northern Venezuela and Colombia and in dry regions of southern Mexico, Honduras and El Salvador (Azevêdo *et al*., 2012).

It is a species that tolerates droughts well, with a large annual regrowth capacity, and is used as an energy source due to the excellent quality of the wood. In addition, it can favor the regeneration of plants that grow under its canopy, thus contributing to the regeneration of eroded soils, as well as being indicated for ecological restoration programs (Santos *et al*., 2011, Paterno *et al*., 2016).

In tropical regions, droughts are often associated with high solar radiation (Gouvêa and Marenco, 2018) which combined with the low capacity of *Caatinga*´s soils, reduce the water storage capacity of this biome. This situation tends to worsen in the face of global climate change that our planet is going through. In their review of climate projections on the Brazilian Northeast, citing some authors, Guimarães *et al*. (2016) report that this is a region with considerable vulnerability to climate change and is subject to changes in the distribution of extreme events, summer events, spatial distribution of rainfall, etc. Hence the need for a better understanding of the physiological strategies developed by the plants of this region to survive under these conditions.

Plant species that inhabit semiarid climate regions respond to water deficit by developing strategies and/or mechanisms for escape or drought tolerance (Araújo, 2005). Because they are subject to long periods of drought, changes occur in physiological, biochemical, molecular and morphological processes due to reduced leaf water potential. Among these physiological modifications, stomata closure assumes a prominent position, causing reduction in stomatal conductance, transpiration and photosynthesis rate, causing a decrease in plant growth (Chaves *et al*., 2003, Fernandes *et al*., 2015). In addition, there is a decrease in protective protein synthesis (Choudhury *et al*., 2017), and as a survival strategy plants can promote osmotic adjustment by accumulation of osmotically compatible solutes, ensuring the maintenance of cell turgidity, avoiding tissue death (Sircelj *et al*., 2007, Nio *et al*., 2011).

Several researchers have developed research to evaluate the effects of water deficit on gas exchange in forest species (Costa *et al*., 2015, Oliveira *et al*., 2016, Moura *et al*., 2016, Oliveira and Gualtieri, 2017). However, there is little research with native plants of *Caatinga* on this subject, and more research is needed to provide this information.

In this sense, this aimed to evaluate the physiological and biochemical responses of black jurema plants submitted to progressive water deficit and subsequent rewatering.

2. Material and Methods

2.1 Plant Growth: Experimental Design

This study took placed in nursery conditions of the Forest Engineering Department, Federal University of Campina Grande, Patos, Paraiba State, Brazil (7°03'34" S and 37°16'30" W, and 242m elevation).

Seeds of *M. tenuiflora* were subjected to integumentary dormancy break according to Bakke *et al*. (2006) and then placed to germinate in conical tubes (125 cm^3) containing the substrate composed of subsoil and cattle manure mixture, 2: 1 ratio. The soil used was analyzed both chemical and physical properties (Table 1). Thirty days after emergence, the seedlings were transferred to plastic pots containing 5 kg of the above substrate. Irrigation was performed daily, trying to keep the substrate humidity close to 70% of the retention capacity, determined by weighing.

The plants were kept in this condition until they reached one year of age, when were separated into two groups, in which one group continued to be normally irrigated (irrigated treatment) and the other had suspended irrigation (water deficit treatment).

The treatment of water stress persisted until it was realized that the photosynthesis (*A*) reached values close to zero, which happened on the seventh day after irrigation interruption. After this, the water supply to the plants resumed, until the photosynthesis rate of the water stress treatment plants reached values close to those observed in the control treatment plants, which occurred three days after rehydration.

Table 1. Chemical and chemical properties of soil used

Chemical analysis	Unity	Value
pH ($CaCl_2$ 0,01 M)	-	5,0
P	$\mu g\ dm^{-3}$	4,5
Ca	$cmol_c\ dm^{-3}$	5,1
Mg	$cmol_c\ dm^{-3}$	1,9
K	$cmol_c\ dm^{-3}$	0,17
Na	$cmol_c\ dm^{-3}$	0,57
H + Al	$cmol_c\ dm^{-3}$	3,1
CTC	%	10,84
V	%	71,4
Physical analysis		
Sand	$g\ kg^{-1}$	780
Silt	$g\ kg^{-1}$	100
Clay	$g\ kg^{-1}$	120

2.2 Water Relation and Gas Exchange Measurements

Throughout the periods of water deficit and rewatering, relative water content (RWC), photosynthesis (*A*), transpiration rate (*E*), stomatal conductance (*g*s), intercellular CO_2 concentration (*c*i) were measured. The water use efficiency (*WUE*) was obtained by the ratio *A/gs*, and *ci/ca* was calculated by ratio in *ci* and CO_2 atmosphere concentration (*ca*).

Plant water status was determined by measurements of relative water content (*RWC*). In order to obtain the *RWC* values, leaves were weighed for fresh mass (FM) determination and then placed in glass dishes for 48 h. After measurement of saturated mass (SM), the plant samples were dried at 70 ℃ for 72 h to determine dry mass (DM). The RWC values were evaluated as *RWC* (%) = [(fw−dw)/(tw−dw)]×100 (Weatherley, 1950), in which fw, dw and tw refer to fresh weight, dry weight and turgid weight, respectively.

Gas exchange measurements were taken from entirely unfolded and healthy leaves (two leaves per plant, in four plants per treatment), exposed and perpendicularly oriented to the sun, from young branches in the middle third of the plant, between 10:00 and 11:00 am, using a portable photosynthesis analyzer LCpro-SD (ADC Bio Scientific Ltd.). All gas exchange measurements were recorded during the typical diurnal range of air temperature, and humidity under our field conditions, and PAR flux was adjusted to 1 200 µmol m^{-2} s^{-1}.

2.3 Data Analysis

All experiments were performed with four replicates, and five plants per replication. Data were subjected to one-way ANOVA, and significant differences determined by the Scott-Knott test ($p < 0.05$), using the ASSISTAT software (Silva and Azevedo, 2002).

3. Results

3.1 Relative Water Content and Gas Exchange

There was a significant difference in *RWC* between treatments from the second day of water deficit imposition, with gradual reduction until the seventh day (Figure 1).

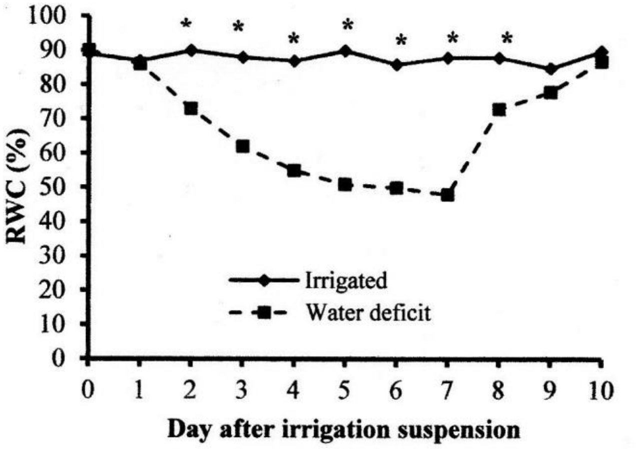

Figure 1. Relative water content (*RWC*) of *M. tenuiflora* plants irrigated and under water deficit. The arrow indicates the day of rewatering

*Differences between treatments on the same day

While irrigated plants maintained a high *RWC* (90%), plants under water deficit reached critical levels on the fourth day, with 55%. This value falls to 48% on the seventh day, corresponding to almost half of the *RWC* of irrigated plants. One day after rewatering, the plants recovered turgidity, reaching 73% *RWC* indicating that there was no damage to cells under low tissue hydration condition, with rapid rehydration with the resumption of water supply. Following the reduction in *RWC*, stomata were affected on the first day of water deficit, with progressive reduction of *E* (Figure 2A), *gs* (Figure 2B), *A* (Figure 2C), and increase *ci* (Figure 2D).

On the seventh day after the beginning of the treatments, irrigated plants presented *E* equal to 4.48 mmol m^{-2} s^{-1}, while in plants under water deficit was 0.043 mmol m^{-2} s^{-1} (Figure 2A), representing a 99% difference. On the day of irrigation suspension, the *E* value was 3.28

mmol $m^{-2} s^{-1}$, reaching 0.043 mmol $m^{-2} s^{-1}$, with 98.6% reduction. Despite the rapid recovery in *RWC* (Figure 1), only on the second day after irrigation that there was an increase in *E*, but much lower than the treatment irrigated. On the last day of the evaluation, three days after the resumption of water supply, there was a total recovery in plant's transpiration.

The *gs* in plants under water deficit decreased progressively as the irrigation suspension period increased, reaching a value equivalent to 94% of the irrigated plants, on the last day after irrigation suspension. After resumption of irrigation, the recovery of this parameter followed the same behavior in *E*.

Regarding *A* in irrigated plants the values ranged from 24.2 to 34.2 µmol $m^{-2}s^{-1}$, while in plants under deficit the variation ranged from 21.1 to 0 µmol $m^{-2}s^{-1}$, respectively on the first and seventh day of the beginning of the treatments (Figure 2C). On the fourth day, theoretically under moderate stress, the plants showed reductions of 54%, 76% and 42% in *gs*, *E* and *A*, indicating that, despite the reduction in stomatal conductance, there was little influence on CO_2 assimilation (Figure 2). However, as the water deficit period increased, stomata closure increased, causing total inhibition in photosynthesis. As with *gs* and *E*, on the third day after rehydration there was a complete recovery in *A*, reaching levels equal to those of irrigated plants, indicating that the water stress imposed was not enough to cause irreversible damage to the stomatal function and the photosynthetic apparatus.

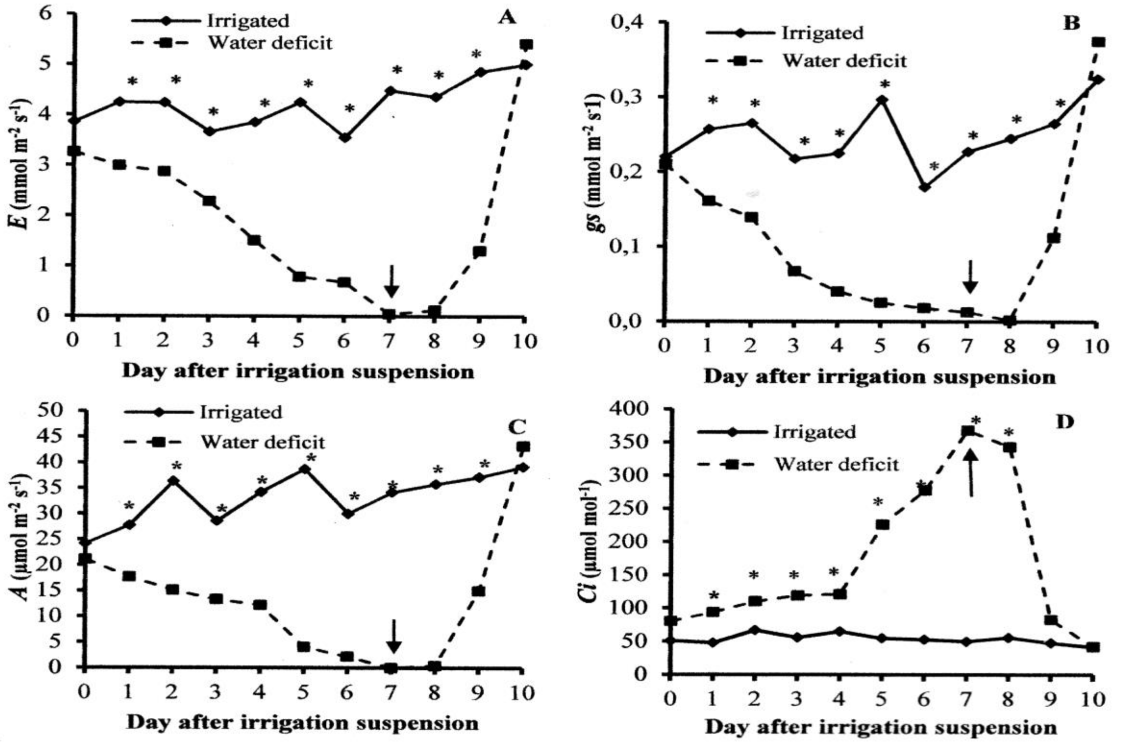

Figure 2. Transpiration (*E*), stomatal conductance (*gs*), photosynthesis (*A*) and intercelular CO_2 concentration (*Ci*) of *M. tenuiflora* plants irrigated and under water deficit. The arrow indicates the day of rewatering

*Differences between treatments on the same day

Irrigated plants maintained *WUE* between 0.1 and 0.17 µmol mol^{-1} (Figure 3A), while plants under water deficit increased from the second to the fourth day, and decreased until 0 µmol mol^{-1} on the seventh day without irrigation.

Due to the behavior observed in *ci* (Figure 2D), the *ci/ca* ratio (Figure 3B) of irrigated plants remained almost constant, whereas in plants under water deficit increased, reaching a maximum of 1.0 on the seventh day after the start of treatments, decreasing after rewatering.

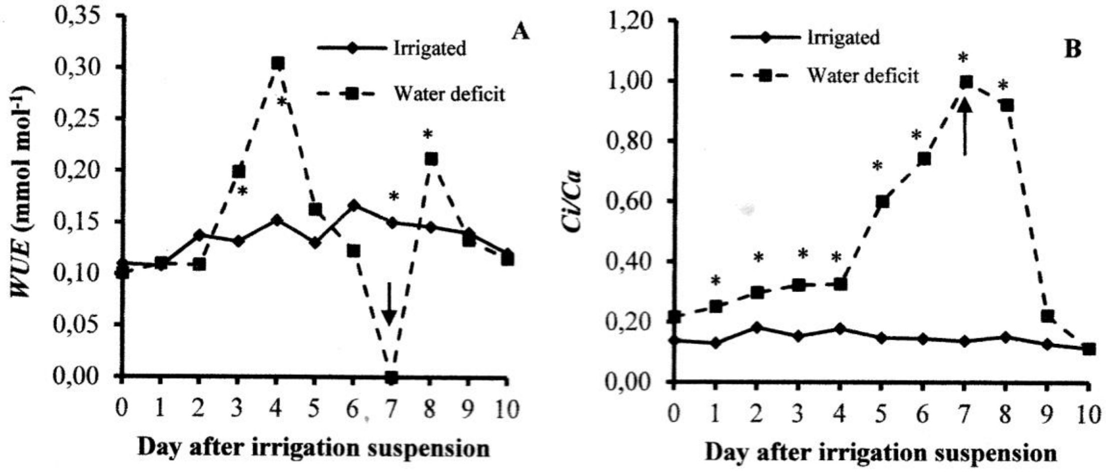

Figure 3. Water use efficiency (*WUE*) and *ci/ca* ration of *M. tenuiflora* plants irrigated and under water deficit. The arrow indicates the day of rewatering

*Differences between treatments on the same day

4. Discussion

According to Pardo (2010), *RWC* 50% is critical to plants, and the adequate value for well-hydrated tissues ranges from 85 to 95%. However, some species adapted to arid and semiarid climate regions can reach this value without tissue death, which may be the case of *M. tenuiflora* plants in this research, since after the resumption of the supply of adequately restored their water status. These results agree with those found in the literature, in *Handroanthus impetiginosus* (Pessoa *et al*. 2017), *Myracrodruon urundeuva* (Costa *et al*., 2015), *Hevea brasiliensis* (Chen *et al*., 2010), and *Quercus pubecens* (Gallé *et al*. ., 2007).

The speed of response to the reduction in water availability varies by species, and the degree of this response directly affects the maintenance of plant tissue water balance. In *H. impetiginosus* seedlings, a 15% reduction in *RWC* was observed on the second day after the water supply was suspended (Pessoa *et al*. 2017). These researchers also reported that at 10 days after irrigation suspension, *RWC* in irrigated and under water deficit plants were 83% and 26%, respectively, resulting in a 69% reduction. In *M. urundeuva* irrigated plants, Costa *et al*. (2015) observed a variation of 82 to 91%, while in plants under water deficit, the *RWC* progressively reduced until reaching the value of 70% on the 12th day of evaluation.

The recovery of *RWC* in *M. tenuiflora* plants after rewatering indicates that stress did not cause irreversible damage to the hydraulic conductivity of the root xylem vessels. Among the effects of water stress are cavitation (Holbrook *et al*., 2001, Otieno *et al*., 2005) and consequent decrease in hydraulic conductivity (Chen *et al*., 2010). However, the phenomenon of cavitation can be immediately neutralized after the resumption of water supply to plants, with recovery of root hydraulic conductivity (Holbrook *et al*., 2001, Otieno *et al*., 2005).

The rapid reduction in *E* and *gs* of plants under water deficit demonstrate the sensitivity of the stomata of this species to water deficit, constituting a survival strategy under adverse water conditions, avoiding excessive loss of tissue water and consequently death by dehydration. The fact that the stomatal mechanism was recovered indicates that the time elapsed from the imposition of water restriction did not cause irreversible damage to the stomata, enabling the recovery of its functioning after plant rehydration. When water supply decreases, guard cells respond to leaf water potential and control their water loss by decreasing transpiration (Chaves *et al*., 2010). These authors add that partial pressure of intercellular CO_2 can control stomatal opening by supplying CO_2 to chloroplast or by CO_2 demand for photosynthesis. The physiological mechanisms of stomata response to water deficit are complex and not yet fully understood (Patakas *et al*., 2005), since they can respond to a series of stimuli, and not all of them are directly related to soil water content, as stomatal sensitivity to vapor pressure deficit (VPD) (Habermann *et al*., 2003). Another stimulus that may regulate the stomatal response is increased cellular abscisic acid (ABA) under water stress conditions (Harris and Outlaw, 1991) or apoplastic ABA on the surface of guard cells, which supposedly cause a reduction in turgor pressure (Assmann, 2003), which in turn leads to stomatal closure (Sousa *et al*., 2006). These factors make stomatal control independent or indirectly related to soil water content.

Decreased photosynthesis under water deficit conditions may occur due to stomatal factors, due to reduced stomatal conductance, restricting gas exchange between the plant and the external environment (Flexas and Medrano, 2002, Flexas *et al*., 2004, Farooq *et al*., 2009), or by non-stomatal factors, due to damage caused to the photosynthetic apparatus (Fu and Huang, 2001) as well as by decreased activity of Calvin Cycle enzymes (Monakhova and Chernyadʹev, 2004). Zhou *et al*. (2013) and Osakabe *et al*. (2014) related a close correlation between water stress and *gs*, which constitutes is one of the most important factors that leads to a decline in *A* during drought conditions (Peeva and Cornic 2009; Zhou *et al*. 2013).

Under mild to moderate water deficits, stomatal closure is one of the first responses of plants, restricting water loss and carbon assimilation (Chaves *et al*., 2003). However, if the deficit condition persists, acclimatization responses such as growth inhibition and osmoregulation are triggered, which are key elements for maintaining the water status of the plant and therefore assimilation of the plant carbon under water scarcity (Chaves *et al*., 2010). In grapevine, maintenance of Calvin Cycle enzymes activity and maximum carboxylation and electron transport rates have been reported under low to moderate water availability (Souza *et al*., 2005). However, as stress intensifies these parameters decline especially in electron transport (Maroco *et al*., 2002, Souza *et al*., 2005), possibly as a result of decreased ATP production (Chaves *et al*., 2010).

The reduction in *WUE* here observed contradicts the results obtained in other studies, where there was an increase in *WUE* under water stress conditions (Diaz-López *et al.*, 2012, Dombroski *et al.*, 2014). While stomatal conductance is more affected than photosynthesis under moderate water stress until the fourth day (Figures 2A and 2B), *WUE* has increased (Figure 3A). Elevation in *WUE* even before complete stomatal closure is a common phenomenon in plants under water stress (Pou *et al*. 2008, Chen *et al*., 2010).

Similar to what happened in *ci* (Figure 2D), in the middle of the water deficit period, between days three and four, the values of *ci/ca* were low, meaning that there was low accumulation of CO_2 in the intercellular spaces, probably because it is being used for photosynthesis, even in smaller quantities (Figure 2C). Thus, non-stomatal factors are believed to play an important role in limiting photosynthesis under water deficit conditions in black jurema plants, as gs decreased and the *ci/ca* ratio increased, as reported (Bacelar *et al.*, 2007). However, some authors state that c*i* values should be carefully analyzed, since stomata opening does not occur evenly due to irregularities in the leaf surface (Bacelar *et al.*, 2007). In addition, *ci* calculated from gas exchange measurements can be overestimated and lead to erroneous conclusions of non-stomatal limitation of photosynthesis (Downton *et al*., 1988).

5. Conclusion

- *Mimosa tenuiflora* plants respond quickly to irrigation suspension, promoting stomata closure, occuring reduction in stomatal conductance, transpiration rate and photosynthesis.

- The water use efficiency of *M. tenuiflora* plants under water deficit remains high for a short period after irrigation water restriction.

- The stress level imposed did not cause irreversible damage to cells and tissue of plants.

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