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Gas exchange of four woody species under salinity and soil waterlogging

Alan D. Lima¹, Carlos H. C. Sousa², Claudivan F. de Lacerda²,
Marlos A. Bezerra³, Evandro N. Silva⁴ & Antônia L. R. Neves²

¹ Faculdade Terra Nordeste. Caucaia, CE. E-mail: alan.lima@fatene.edu.br (Corresponding author)

² Universidade Federal do Ceará/Departamento de Engenharia Agrícola. Fortaleza, CE. E-mail: sousaibiapina@yahoo.com.br; cfeitosa@ufc.br; leilaneves7@hotmail.com

³ Embrapa Agroindústria Tropical/Laboratório de Fisiologia Vegetal. Fortaleza, CE. E-mail: marlos.bezerra@embrapa.br

⁴ Faculdade de Educação, Ciências e Letras do Sertão Central. Quixadá, CE. E-mail: evandro.silva@uece.br

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ABSTRACT

The objective of this study was to evaluate gas exchanges in seedlings of forest species grown in saline soils and subjected to soil waterlogging cycles. The experimental design was completely randomized in a factorial arrangement, with four forest species: *Myracrodruon urundeuva* Fr Allemão, *Mimosa caesalpiniiifolia* Benth, *Tabebuia impetiginosa* (Mart. ex. DC.) Standl and *Azadirachta indica* A. Juss, two soil salinity levels (1.2 and 8.6 dS m⁻¹) and two water regimes (with and without waterlogging). Measurements of stomatal conductance, transpiration and CO₂ assimilation rate were performed before and after each waterlogging period. The interaction of the highest saline level (8.6 dS m⁻¹) and waterlogging caused greater reductions in leaf gas exchange, except for *Mimosa caesalpiniiifolia* Benth. *Tabebuia impetiginosa* (Mart. ex. DC.) Standl was the species with highest sensitivity to both studied factors of stress.

Palavras-chave:

fotossíntese
estresse salino
excesso de água
Caatinga

Trocas gasosas de quatro espécies lenhosas sob salinidade e encharcamento do solo

RESUMO

Objetivou-se, com este trabalho, avaliar as trocas gasosas de mudas de espécies florestais cultivadas em solos salinos e submetidas a ciclos de encharcamento do solo. O delineamento experimental foi inteiramente casualizado em esquema fatorial, com quatro espécies florestais *Myracrodruon urundeuva* Fr Allemão, *Mimosa caesalpiniiifolia* Benth, *Tabebuia impetiginosa* (Mart. ex. DC.) Standl e *Azadirachta indica* A. Juss, dois níveis de salinidade do solo (1,2 e 8,6 dS m⁻¹) e dois regimes hídricos (com e sem encharcamento do solo). Foram realizadas medições, antes e depois de cada período de encharcamento, da condutância estomática, transpiração e taxa de assimilação de CO₂. A interação do maior nível salino (8,6 ds m⁻¹) e do encharcamento do solo causou maiores reduções nas trocas gasosas, exceto para as mudas de *Mimosa caesalpiniiifolia* Benth. *Tabebuia impetiginosa* (Mart. ex. DC.) Standl foi a espécie que apresentou maior sensibilidade aos dois fatores de estresse estudados.



INTRODUCTION

Extensive irrigated areas worldwide have shown reduction in production due to the excess of salts (Leal et al., 2008). Salt-affected areas occur all over the world, especially in regions with arid and semi-arid climate, where irrigation is fundamental for a successful agriculture. It is estimated that 20% of irrigated areas are affected by salinization, resulting from the accumulation of salts caused by irrigation (Aragüés et al., 2011). This advancement in irrigation with the use of low-quality water in semi-arid regions and in marginal land areas has increased the accumulation of salts in the soils and, consequently, their degradation (Ribeiro et al., 2016).

Another factor that contributes to the increase of salinity is the excess of water, caused by inadequate irrigation management. Waterlogging periods in which the water depth covers the soil at higher levels can cause death of the seedlings and also produce differences in their structure and density (Soares & Oliveira, 2009).

It is common knowledge that some forest species, native and/or exotic, are physiologically tolerant to the most varied types of stress. Thus, studies on the physiological responses of plants under stress conditions can generate useful information for the reforestation of degraded areas.

Physiological evaluations, such as gas exchanges, can be performed in a direct and non-destructive manner and are related to the excess of salts and saturation or waterlogging of the soil. In this context, this study aimed to evaluate gas exchanges in seedlings of four forest species cultivated in saline soils and under soil waterlogging cycles.

MATERIAL AND METHODS

The experiment was carried out at the Center of Teaching and Research on Urban Agriculture (NEPAU) of the Department of Plant Science of the Federal University of Ceará - UFC, Fortaleza, CE, located at 3° 44' S and 38° 33' W, at altitude of 20 m, from October 27, 2013, to February 25, 2014.

To compose the treatments with levels of salts, samples of a soil classified as Fluvic Neosol (EMBRAPA, 2013) were collected in different points of the Morada Nova Irrigation District. The points were selected based on in-situ analysis of soil electrical conductivity (EC), in the layer of 0-20 cm, using a Wet Jet sensor (Delta T - Devices, Cambridge, England). After sampling, the soil was pounded to break up clods and sieved through a 5-mm mesh. Then, the EC of the saturated soil was measured, resulting in two saline treatments (1.2 and 8.6 dS m⁻¹).

Forest species were used in the experiment, three of which are native to the Caatinga: 'Aroeira' (*Myracrodruon urundeuva* Fr Allemão), 'Sabiá' (*Mimosa caesalpinifolia* Benth) and 'Ipê roxo' (*Tabebuia impetiginosa* (Mart. ex. DC.) Standl), and one exotic species, 'Nim' (*Azadirachta indica* A. Juss). The seedlings were produced in greenhouse with 50% shading through sowing on polystyrene trays with 128 cells and substrate of sand + earthworm humus at proportion of 2:1, where they remained for 20 days, being daily irrigated through a micro-sprinkler system using well water with EC of 0.7 dS m⁻¹.

At 20 days after sowing, the seedlings were selected according to the uniformity and then transplanted to 8-L buckets containing in their profiles a 5-cm bottom layer of crushed stone and each soil with the respective levels of salinity. To reduce the impact of the direct contact between the root system of the seedlings and the saline soil, the holes of each pot received an adequate volume of washed river sand. A period of 20 days after transplanting (DAT) without the treatment of soil waterlogging was adopted. After this adaptation period, the plants remained in the pots until 100 DAT, being daily irrigated through a micro-sprinkler system.

The experimental design was completely randomized with four replicates in a 4 x 2 x 2 factorial scheme, relative to four forest species ('Nim', 'Aroeira', 'Ipê' and 'Sabiá'), two soil salinity levels, low and high (1.2 and 8.6 dS m⁻¹, respectively) and two water regimes (with and without soil waterlogging), totaling 64 experimental units.

To study the effect of waterlogging, part of the pots was maintained with moisture content above field capacity. Three waterlogging cycles were applied plus one cycle of recovery, with duration of 3 days each, simulating the occurrence of three floods. The first waterlogging cycle occurred at 21 DAT and continued up to 24 DAT; after this waterlogging period, excess water was drained and plants remained in this condition for 15 days, when a new waterlogging cycle was applied, at 39 DAT and another at 58 DAT. For the treatment without waterlogging, soil moisture was maintained within the optimum range for the development of the species, during all the experiment.

Before and after each waterlogging period, stomatal conductance (gs), transpiration (E) and CO₂ assimilation rate (A) were measured in fully expanded leaves, using a portable infrared gas analyzer - IRGA (model LCI, ADC BioScientific, England). The measurements were taken between 8 and 11 a.m. under saturating light condition obtained with an attached artificial source (approximately 1,200 μmol m⁻² s⁻¹), at room temperature and room CO₂ concentration.

The results were subjected to analysis of variance by F test and the means were compared by Tukey test at 0.05 probability level using the program Assistat, version 7.6 beta (Silva & Azevedo, 2016).

RESULTS AND DISCUSSION

Table 1 shows the representation of the analysis of variance (ANOVA) for the variables stomatal conductance (gs), CO₂ assimilation rate (A), transpiration (E) before (BEF) and after (AFT) waterlogging, in relation to the factors forest species (Factor A), salinity (Factor B) and water regime (Factor C). It is noted that the species showed different responses regarding leaf gas exchanges and that these alterations were influenced by the interactions with the factors salinity and soil waterlogging.

According to the mean values of stomatal conductance (gs) of plants in the soil before waterlogging (Figure 1A), the species 'Aroeira' and 'Sabiá' exhibited superior values of gs, 0.189 and 0.213 mol m⁻² s⁻¹, respectively, but without differing from one another. On the other hand, the species 'Nim' and 'Ipê' showed inferior values, respectively 0.127 and 0.111 mol m⁻² s⁻¹.

Table 1. Summary of the analysis of variance for stomatal conductance (gs), CO₂ assimilation rate (A) and transpiration (E) before (_{BEF}) and after (_{AFT}) soil waterlogging cycles (C), in seedlings of four woody species (A) cultivated in soil with low and high salinity (B)

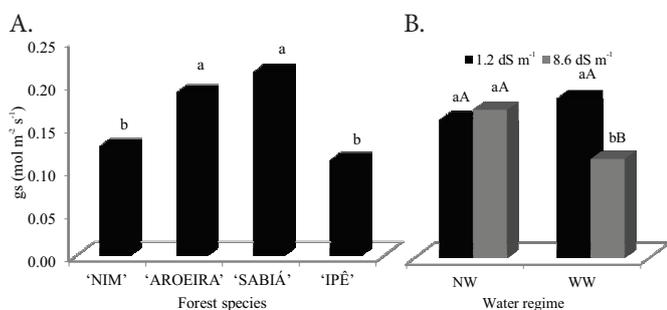
SV	DF	Mean square					
		GS _{BEF}	GS _{AFT}	A _{BEF}	A _{AFT}	E _{BEF}	E _{AFT}
(A)	3	0.038**	0.072**	17.84**	29.58**	14.16**	3.22**
(B)	1	0.014**	0.006 ^{ns}	6.16 ^{ns}	7.89*	0.15 ^{ns}	0.24 ^{ns}
(C)	1	0.004 ^{ns}	0.021**	13.33**	45.98**	0.64 ^{ns}	0.96**
A x B	3	0.001 ^{ns}	0.002 ^{ns}	1.57 ^{ns}	4.67**	2.01**	0.40**
A x C	3	0.003 ^{ns}	0.014**	1.31 ^{ns}	14.36**	2.44**	2.17**
B x C	1	0.028**	0.000**	20.65**	0.57 ^{ns}	3.96**	0.09 ^{ns}
A x B x C	3	0.001 ^{ns}	0.005**	0.82 ^{ns}	4.44*	1.02 ^{ns}	0.64**
Treatment	15	0.012**	0.020**	6.98**	14.24**	4.24**	1.37**
Residual	48	0.001	0.001	1.59	1.1	0.44	0.06
Total	63	-	-	-	-	-	-

** , * and ^{ns} – Significant at 0.01 and 0.05 probability levels and not significant by F test, respectively

Figure 1B shows the responses for gs as a function of the interaction salinity versus water regime before the waterlogging cycles. In the treatment with no waterlogging (NW), there are no differences in the situations with low (1.2 dS m⁻¹) and high (8.6 dS m⁻¹) soil salinity, but the increase in salinity caused reduction of 38.47% in stomatal conductance, when plants were also subjected to the cycles of soil waterlogging (WW).

For Olivella et al. (2000), under flood conditions the abscisic acid and cytokinin can work as messengers of the plant under stress, regulating stomatal opening, which may have occurred in the treatment with 8.6 dS m⁻¹ under waterlogging conditions.

According to the results in Table 2, the species 'Sabiá' showed highest values of gs, regardless of the cultivation conditions. The species 'Nim' was not influenced by the waterlogging cycles, but showed lower values at the highest salinity level, which may evidence tolerance to waterlogging. 'Aroeira' and 'Ipê' were influenced by soil waterlogging, especially under high salinity conditions, with greater reductions in gs for 'Ipê'. For this species, the lowest and highest values were recorded in the treatment with highest and lowest stress, respectively, 8.6WW (high salinity and with waterlogging) with absolute values on the order of 0.048 mol m⁻² s⁻¹, and 1.2NW (low salinity and without waterlogging) with values of 0.134 mol m⁻² s⁻¹, thus showing statistical difference with reduction on the order of 64%.



Means followed by the same letter do not differ statistically by Tukey test ($p > 0.05$) (A); Bars with the same uppercase letters, for salinity, and by the same lowercase letters, for water regime, do not differ statistically by Tukey test ($p > 0.05$) (B)

Figure 1. Stomatal conductance (gs) for the studied species (A) and for the interaction Salinity versus Water regime (B), before the cycles of soil waterlogging. NW = without waterlogging; WW = with waterlogging

Table 2. Stomatal conductance (gs) after the soil waterlogging cycles as a function of the interaction between species, salinity and water regime

Species	gs (mol m ⁻² s ⁻¹)			
	1.2NW	1.2WW	8.6NW	8.6WW
'Nim'	0.177 abA	0.149 bA	0.113 bA	0.111 bA
'Aroeira'	0.198 abAB	0.136 bBC	0.229 aA	0.078 bC
'Sabiá'	0.252 aA	0.246 aA	0.221 aA	0.298 aA
'Ipê'	0.134 bA	0.083 bAB	0.115 bAB	0.048 bB

1.2NW - Low salinity without waterlogging; 1.2WW - Low salinity with waterlogging; 8.6NW - High salinity without waterlogging; 8.6WW - High salinity with waterlogging; Means followed by the same letter, uppercase in the row and lowercase in the column, do not differ statistically

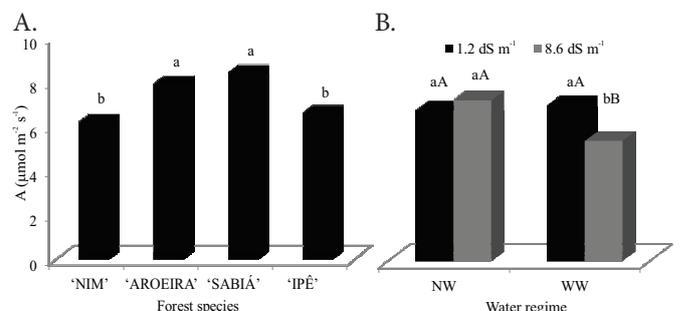
In general, plants subjected to the regime of soil waterlogging with low or high salinity exhibited lower values of the studied variable, in comparison to the regime with no soil waterlogging. These results were more expressive negatively, because at the moment of the readings plants were under the final conditions of the waterlogging cycle, different from the readings taken before the beginning of the waterlogging.

Part of the results found in this study can be explained by the comments of Herrera et al. (2008), who reported that the reduction of stomatal conductance in plants maintained in saturated or waterlogged soils, combined with the high CO₂ concentration found in the intercellular spaces of the mesophyll, suggests that stomatal closure is not the only cause of reduction in the photosynthetic rate. Probably, waterlogging must also affect RuBisCO activity, besides causing damages to photosystem II.

In studies conducted with *Cecropia pachystachya*, which is a species of wet soils, Batista et al. (2008) reported reduction in stomatal conductance and CO₂ assimilation rate when subjected to waterlogging. For these authors, the increase in the sclerophylly index of the leaves of plants under waterlogging possibly caused reduction in water loss, contributing so that there was not a greater loss of stomatal conductance and photosynthetic rate.

Figure 2A shows the values of CO₂ assimilation rate (A) as a function of the analyzed species, before the waterlogging to which plants were subjected. The species with highest A values were 'Sabiá', with 8.4 μmol m⁻² s⁻¹, and 'Aroeira', with 7.9 μmol m⁻² s⁻¹, with superiority in relation to the species 'Ipê' and 'Nim'.

Figure 2B illustrates the interaction of salinity treatment in the soil with and without waterlogging for the studied



Means followed by the same letter do not differ statistically by Tukey test ($p > 0.05$) (A); Bars with the same uppercase letters, for salinity, and by the same lowercase letters, for species, do not differ statistically by Tukey test ($p > 0.05$) (B)

Figure 2. CO₂ assimilation rate (A) for the studied species (A) and for the interaction Salinity versus Water regime (B), before the cycles of soil waterlogging

woody species. It is noted that the increase in salinity did not influence CO_2 assimilation rate in plants not subjected to waterlogging, but there was significant reduction when subjected to high salinity and waterlogging, causing mean reduction in photosynthetic rate on the order of 23%.

According to the results, soil waterlogging was the factor with highest contribution to the reduction in photosynthetic rates, because salinity individually did not interfere in a more harmful way with this process. These results can be justified according to Chen et al. (2011), who report that plants under waterlogging tend to exhibit a reduction in photosynthesis, which is the main cause of growth reduction in plants under this type of stress. Barddal (2006) observed that the photosynthetic rate also decreased in plants subjected to waterlogged soil, and with 15 days of waterlogging the reduction was more pronounced than at two and five days.

The similarity of the behavior for photosynthetic rate (Table 3) and stomatal conductance (Table 2), in response to the interaction between the three factors, indicates that the reduction in CO_2 assimilation rate can be related more directly to stomatal closure.

As observed for g_s , the highest reductions in CO_2 assimilation (A) occurred in plants of the treatments with highest salinity level and under waterlogging conditions, with more expressive reductions in 'Ipê' plants.

It should be pointed out that other studies have identified alterations in non-stomatal aspects, such as effects on enzymes of the Calvin cycle or alteration in the photochemical reactions (Herrera et al., 2008), and possible discrepancies can be related to the intensity and duration of the stress.

According to Silva et al. (2011), not only prolonged exposure to salts leads to alterations in the water status of the

Table 3. CO_2 assimilation rate (A) as a function of the interaction between species, salinity and soil water regime after waterlogging cycles

Species	A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)			
	1.2NW	1.2WW	8.6NW	8.6WW
'Nim'	7.54 abA	7.26 aAB	5.81 bAB	5.34 Bb
'Aroeira'	8.66 aA	6.41 aB	9.33 aA	4.37 bcC
'Sabiá'	7.94 abA	6.97 aA	7.51 abA	8.91 Aa
'Ipê'	6.47 bA	3.95 bBC	5.91 bAB	2.40 Cc

1.2NW - Low salinity without waterlogging; 1.2WW - Low salinity with waterlogging; 8.6NW - High salinity without waterlogging; 8.6WW - High salinity with waterlogging; Means followed by the same letter, uppercase in the row and lowercase in the column, do not differ statistically

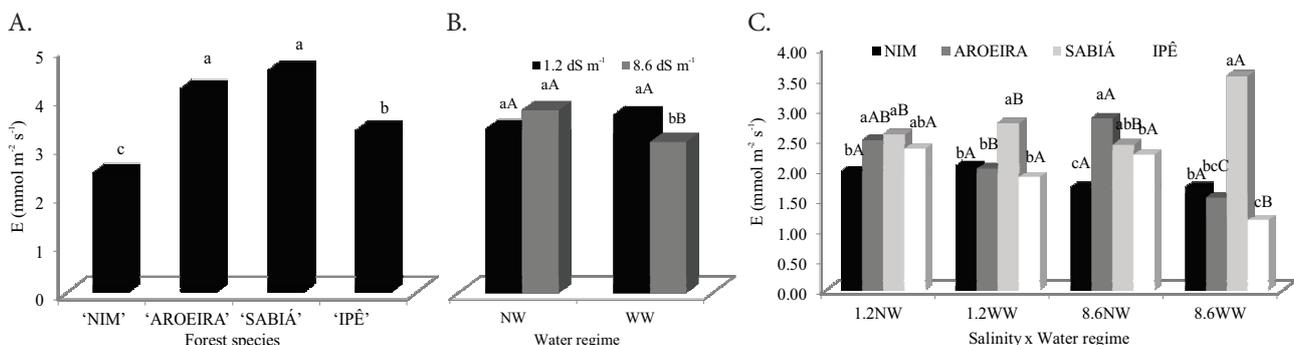
plants, inducing stomatal closure and consequently limitation in CO_2 entry, but also high concentrations of ions such as Na^+ and Cl^- have been pointed as the main causes of damages to the structures of enzymes and membranes, directly interfering with photosynthesis. This occurs because salt stress causes decrease in the turgor potential of the leaf tissues (Taiz & Zeiger, 2013), besides stomatal closure, increase of resistance to CO_2 diffusion and decrease of photosynthetic rate (Chaves et al., 2009). In the present study, however, the effects of salinity were observed only on plants under waterlogging.

The absence of significant differences obtained before and after waterlogging, directly in the photosynthetic process and indirectly through stomatal closure, is an indication of the recovery capacity in the levels of photosynthetic rate after the waterlogging period. Thus, these possible recoveries that occurred immediately after the drainage periods were the ones which allowed the plants to survive even under waterlogging regime, showing similar values between the moments before and after soil waterlogging.

The transpiration of the species (Figure 3A) revealed similar behavior to those of stomatal conductance (Figure 1A) and CO_2 assimilation rate (Figure 2A), with the highest values for the species 'Sabiá' ($4.56 \text{ mmol m}^{-2} \text{ s}^{-1}$) and 'Aroeira' ($4.19 \text{ mmol m}^{-2} \text{ s}^{-1}$), both statistically equal, and lowest values for the species 'Ipê' and 'Nim', which in turn were statistically different.

According to Figure 3B, there was statistical difference only in the treatments with different salinity levels (1.2 and 8.6 dS m^{-1}), when plants were subjected to soil waterlogging.

This similarity between the responses of E and g_s is evidenced by the data of the interaction, as shown in Figure 3C, compared with those of g_s in Table 2. Lira et al. (2013), evaluating gas exchanges of *Lonchocarpus sericeus* (Poir.) D.C. plants under waterlogging regimes, observed that water excess in the soil caused reduction in transpiration. The authors justify that the reduction in the values of gas exchange variables at 90 days, in both treatments (field capacity and waterlogged), may have been due to the increase in leaf temperature caused by the increase in the temperature of the environment. According to Sultana et al. (1999), regardless of the type of limitation, besides affecting photosynthesis, salinity can alter the relative water content and water potential of the leaves, stomatal conductance, transpiration and leaf temperature.



Means followed by the same letter do not differ statistically by Tukey test (A); Bars with the same uppercase letters, for salinity, and by the same lowercase letters, for species, do not differ statistically by Tukey test (B); Means followed by the same uppercase letter between treatments and lowercase letter in the treatment, do not differ statistically (C)

Figure 3. Transpiration (E) for the studied species (A), for the interaction Salinity versus Water regime (B) before waterlogging cycles and for species, salinity and water regime after waterlogging cycles (C)

CONCLUSIONS

1. Soil waterlogging was the factor that most contributed to the reduction in leaf gas exchanges.
2. The gas exchanges of the plants were more inhibited by the highest salinity and soil waterlogging, except in 'Sabiá' seedlings.
3. The species 'Ipê roxo' was the most sensitive to the evaluated stress factors.

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