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Gas exchange and organic solutes in forage sorghum genotypes grown under different salinity levels

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Key words:

salt stress
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Sorghum bicolor (L.) Moench

ABSTRACT

Adaptation of plants to saline environments depends on the activation of mechanisms that minimize the effects of excess ions on vital processes, such as photosynthesis. The objective of this study was to evaluate the leaf gas exchange, chlorophyll, and organic solute in ten genotypes of forage sorghum irrigated with solutions of different salinity levels. The experiment was conducted in a randomized block design, in a 10 x 6 factorial arrangement, with three replications, using ten genotypes - F305, BRS-655, BRS-610, Volumax, 1.015.045, 1.016.005, 1.016.009, 1.016.013, 1.016.015 and 1.016.031 - and six saline solutions, with electrical conductivity (EC_w) of 0, 2.5, 5.0, 7.5, 10 and 12.5 $dS\ m^{-1}$. The photosynthetic activity in forage sorghum plants reduces with increasing salinity, and this response was found in the ten genotypes evaluated. The chlorophyll and protein contents were not affected by salinity, whereas carbohydrates and amino acid contents increased with increasing EC_w . Soluble sugars are essential for osmoregulation of forage sorghum due to its high content in leaves.

Palavras-chave:

salinidade
fotossíntese
clorofila
Sorghum bicolor (L.) Moench

Trocas gasosas e solutos orgânicos em genótipos de sorgo forrageiro sob diferentes níveis de salinidade

RESUMO

A adaptação das plantas a ambientes salinos depende da ativação de mecanismos que minimizam os efeitos do excesso de íons sobre processos vitais como a fotossíntese. O objetivo desse trabalho foi avaliar as trocas gasosas, teores de clorofila e de solutos orgânicos em genótipos de sorgo forrageiro irrigados com soluções de diferentes níveis de salinidade. Utilizou-se o delineamento experimental em blocos casualizados dispostos em esquema fatorial 10 x 6, considerando dez genótipos: 'F305', 'BRS 655', 'BRS-610', 'Volumax', 1.015.045, 1.016.005, 1.016.009, 1.016.013, 1.016.015 e 1.016.031; e soluções com seis valores de condutividade elétrica (CE_a): 0; 2,5; 5,0; 7,5; 10 e 12,5 $dS\ m^{-1}$, utilizando-se três repetições. O aumento da salinidade influenciou diretamente a redução da atividade fotosintética do sorgo forrageiro, sendo essas respostas semelhantes para os dez genótipos estudados. Os índices de clorofila e teores de proteínas não foram afetados com a salinidade, enquanto que os teores de açúcares solúveis totais, açúcares redutores e aminoácidos foram crescentes com o aumento da CE_a . Devido a sua concentração nas folhas, os açúcares solúveis devem exercer papel predominante na osmorregulação dos genótipos de sorgo forrageiro.



INTRODUCTION

The edaphoclimatic characteristics of the Brazilian semiarid region favor the accumulation of salts in the soil and water sources, causing a stress condition for plants (Medeiros et al., 2010). Plants subjected to salt stress can reduce their photosynthetic rate because of stomatal closure, which limits CO₂ availability and interferes in the photosynthetic pigment synthesis, such as chlorophyll (Jamil et al., 2007). This response promotes disturbances on enzyme systems responsible for producing and distributing photosynthetic assimilates (Munns & Tester, 2008).

Tolerant plants have several biochemical and molecular mechanisms to cope with salt stress, such as synthesis and accumulation of organic compounds—compatible solutes (Parida & Das, 2005). Compatible solutes are grouped mainly into simple and complex sugars, sugar alcohols, and quaternaries derived from amino acids; accumulations of compatible solutes differ between organisms, even between plant species (Oliveira et al., 2010).

Sorghum bicolor (L) Moench. is a crop species that presents C₄ mechanism, and is one of the most versatile and efficient species in terms of photosynthetic mechanism (Berenguer & Faci, 2001). This contributes to its greater resistance to adverse conditions. The genetic variability of forage sorghum causes different physiological responses to stresses between genotypes. Therefore, the objective of this study was to evaluate the leaf gas exchange, chlorophyll, and organic solute in ten genotypes of forage sorghum irrigated with solutions of different salinity levels.

MATERIAL AND METHODS

The experiment was conducted in a greenhouse located in Petrolina, Pernambuco, Brazil (9° 9' S, 40° 22' W), using ten forage sorghum genotypes—F305, BRS-655, BRS-610, Volumax, 1.015.045, 1.016.005, 1.016.009, 1.016.013, 1.016.015 and 1.016.031. Seeds of the genotypes were sown in 8 L plastic pots filled with soils sieved in 4 mm mesh sieves. The drainage was controlled by a layer of approximately two inches of gravel placed at the bottom of the pots, which were perforated and connected to hose collectors. The soil used was classified as Arenic Haplult, with 84.7% of sand, 13.5% of silt, and 1.8% of clay.

Thinning was performed two weeks after sowing, leaving two plants per pot. Then, the treatments with saline solutions - electrical conductivity (EC_w) of 0, 2.5, 5.0, 7.5, 10 and 12.5 dS m⁻¹ - were applied. The saline solutions were prepared with NaCl, CaCl₂·2H₂O, and MgSO₄·7H₂O salts to obtain the equivalent ratio of 7:2:1 (Na:Ca:Mg) (Aquino et al., 2007). The experiment was conducted in a randomized block design, in a 10 x 6 factorial arrangement, with three replications, using ten forage sorghum genotypes and six saline solutions. These solutions were applied manually every two days to maintain the soil moisture close to the field capacity and with a leaching fraction of approximately 0.15.

A nutrient solution was applied to the soil to correct nutritional lacks, which consisted of (mg L⁻¹): 160 of N, 400

of P, 210 of K, 180 of S, 0.81 of B, 4.0 of Zn, 3.66 of Mn, 1.33 of Cu, 0.15 of Mo and 0.10 of Fe (Novais et al., 1999). The nutrients sources were (NH₄)₂SO₄, NaH₂PO₄, KH₂PO₄, H₃BO₃, CuSO₄·5H₂O, (NH₄)₆Mo₇O₂₄·4H₂O, MnSO₄·H₂O, ZnSO₄·7H₂O, FeSO₄·7H₂O and Na₂EDTA. The nutrient solution was applied after thinning in three times with fifteen-day intervals.

Leaf gas exchange, and chlorophyll a and b were measured after 60 days under salt stress, and +3 leaves (third expanded leaf from the apex) were collected and frozen in liquid nitrogen for the further analyses of total soluble sugars, reducing sugars, total free amino acid, and total soluble proteins.

Leaf gas exchange was evaluated using an infrared gas analyzer system (IRGA, Li-6400), in the youngest completely expanded leaf of each plant, under a saturating photosynthetic photon flux density of 1800 μmol m⁻² s⁻¹. The variables analyzed were photosynthesis (A), stomatal conductance (gs), transpiration (E) and leaf temperature (Tf). Instantaneous water use efficiency (WUE) and intrinsic water use efficiency (IWUE) were assessed from the A to E ratio, and A to gs ratio, respectively. Chlorophyll a and b were determined from readings in three points of the +3 leaves, using the CFL ClorofiLOG 1030.

Organic solutes were extracted by macerating 0.3 g of fresh leaf homogenized in 4.0 mL of phosphate buffer (1.0 mol L⁻¹, pH 7.0) prepared with potassium dihydrogen phosphate (KH₂PO₄) and sodium hydrogen phosphate (Na₂HPO₄) solutions. The material was centrifuged at 2.000 x g, at 23 °C for 20 min. The supernatant was collected to analyze the total soluble sugars, reducing sugars, total free amino acids, and total soluble proteins.

Soluble sugars were determined according to the Antrona method (Yemm & Willis, 1954), and reducing sugars were quantified by using 3,5-dinitrosalicylic acid (Miller, 1959). Total free amino acids were determined by the ninhydrin assay (Yemm & Cocking, 1955), and total soluble proteins were quantified according to the Bradford's method (Bradford, 1976).

The data were subjected to analysis of variance using the Sisvar 5.0 program. When the EC_w factor was significant, the data were subjected to regression models and tested at 1% probability (t test). The Scott Knott test at 5% probability was used to compare the genotypes.

RESULTS AND DISCUSSION

The analysis of variance showed no significant interactions between genotypes and salinity effects, which allows an independent analysis of these factors. Irrigation with salinity solution caused significant effect on leaf gas exchange and leaf organic solute contents, but did not affect the chlorophyll a and b contents in the forage sorghum genotypes evaluated. The genotypes showed similar results of net photosynthesis (A) regardless of the salinity level (Table 1), except F305, which showed the lowest A.

The lowest net photosynthesis of the genotype F305 might be related to its limitation in stomatal opening, as shown by lower stomatal conductance (gs), which caused low water loss through the transpiration process. The stomatal closure is an

Table 1. Physiological analysis of leaves of ten forage sorghum genotypes subjected to different salinity levels

Genotypes	A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	gs ($\text{mol m}^{-2} \text{s}^{-1}$)	E ($\text{mmol m}^{-2} \text{s}^{-1}$)	Tf ($^{\circ}\text{C}$)	WUE	IWUE
F305	16.0 b	0.061 b	1.57 c	31.8 a	9.7 a	258.6 a
BRS-655	27.8 a	0.158 a	3.41 a	31.5 b	8.8 a	202.2 a
BRS-610	29.3 a	0.150 a	3.18 a	31.3 b	9.2 a	207.0 a
Volumax	25.0 a	0.116 b	2.64 b	31.6 a	10.8 a	264.1 a
1.015.045	28.1 a	0.179 a	3.56 a	31.3 b	8.3 a	186.5 a
1.016.005	22.0 a	0.097 b	2.21 b	31.6 a	12.3 a	315.8 a
1.016.009	23.8 a	0.111 b	2.53 b	31.8 a	9.7 a	240.9 a
1.016.013	26.5 a	0.136 b	2.88 b	31.6 a	10.7 a	262.7 a
1.016.015	23.9 a	0.110 b	2.46 b	31.7 a	11.1 a	280.6 a
1.016.031	26.3 a	0.127 b	2.81 b	31.7 a	12.3 a	312.1 a

A = Net photosynthesis; gs = Stomatal conductance; E = Transpiration; Tf = Leaf temperature; WUE = Instantaneous water use efficiency; IWUE = Intrinsic water use efficiency. Means followed by the same letter in the columns do not differ by the Scott Knott test at 0.05 probability

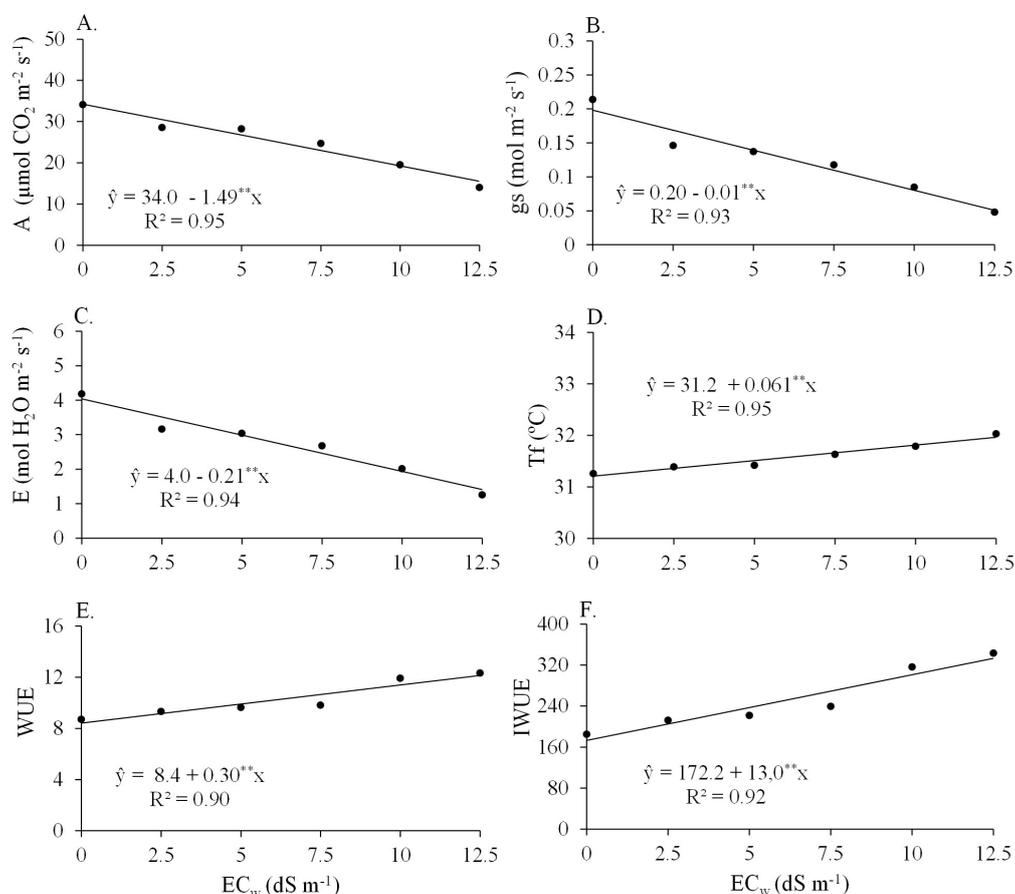
adaptive mechanism of plants to prevent excessive loss of water, especially under stress conditions (Wang et al., 2016). However, this mechanism affects the photosynthetic activity, and limits the entry of CO_2 through stomatal pores; this may cause a reduction in the photoassimilate production, affecting growth and productivity, as already observed in sorghum-sudangrass crops (Feijão et al., 2011).

The average photosynthesis found in the genotypes, except F305, was close to that commonly found for forage sorghum. Miranda et al. (2013) found photosynthesis rates of 25 to 35 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in forage sorghum, and no significant changes in these rates after application of 75 mM salt solutions for three and seven days were observed. Kakani et al. (2011) found photosynthesis rates of 35 to 45 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in grains of sorghum

plants that were not subjected to environmental stresses. Similar result was found by Xie & Su (2012), who evaluated sweet sorghum leaves in peak radiation hours, and under non-apparent stress.

The BRS-655, BRS-610 and 1.015.045 genotypes had higher stomatal conductance (gs), which promoted higher transpiration rates (E), and consequently lower leaf temperature (Tf). However, the higher gs of these genotypes were not followed by a significant increase in photosynthesis. Although the genotypes had differences in A, gs, and E, they had similar results of instantaneous water use efficiency (WUE), and intrinsic water use efficiency (IWUE).

Regarding the effect of salinity on gas exchange, the A, gs, and E had linear reductions with increasing EC_w (Figure 1).



Regression ** significant at 0.01 probability (t test)

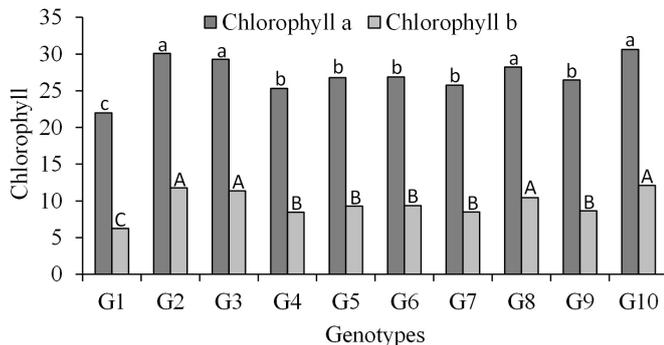
Figure 1. A = Photosynthesis rate (A), gs = Stomatal conductance (B), E = Transpiration (C), Tf = Leaf temperature (D), WUE = Instantaneous water use efficiency (E), and IWUE = Intrinsic water use efficiency (F) in different sorghum genotypes, after 60 days of irrigation with saline solutions of different electrical conductivity levels

Long exposure to salts causes changes in the plant water status, stomatal closure and, consequently, limitation of mesophyll conductance to CO₂ (Silva et al., 2011). Moreover, high concentrations of ions, such as Na⁺ and Cl⁻, have been reported as the cause of damage to enzyme and membrane structures, affecting directly the photosynthesis. Reductions of gs with consequent reductions of A and E were also found in *Jatropha curcas* (Sousa et al., 2012) and common beans (Souza et al., 2011).

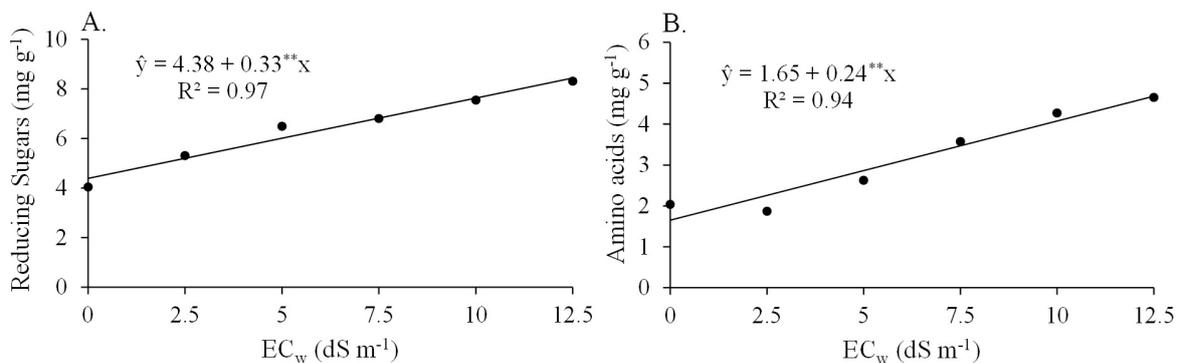
The A (Figure 1A), gs (Figure 1B) and E (Figure 1C) reduced with salinity, and the Tf (Figure 1D), WUE (Figure 1E) and IWUE (Figure 1F) increased gradually with increasing EC_w. This denotes the ability of this crop to adapt to saline stress and maintain a positive photosynthesis rate, even under conditions that limits water absorption.

This response may be related to the C₄ metabolism of forage sorghum plants, which results in high rates of photosynthesis under conditions of temporary reduction in the availability of CO₂ caused by stomatal closure (Taiz & Zeiger, 2013). Fernandes et al. (2010) reported that plants with high WUE might present high tolerance to salinity due to their great water loss control, and reduction of the toxic ion flow to plant shoot after limiting transpiration.

Different chlorophyll a and b contents were found only between genotypes (Figure 2), denoting that this variable is intrinsic to each genotype, and not related to the salt effects on the plants. Different results were found by Lacerda et al. (2003), who evaluated two fodder sorghum varieties.



Bars with the same lowercase letters for chlorophyll a content, and the same uppercase letters for chlorophyll b content do not differ among genotypes by the Scott Knott test at 5% probability (Figure 2). Chlorophyll a and b contents in leaves of ten forage sorghum genotypes - F305 (G1), BRS-655 (G2), BRS-610 (G3), Volumax (G4), 1.015.045 (G5), 1.016.005 (G6), 1.016.009 (G7), 1.016.013 (G8), 1.016.015 (G9) and 1.016.031 (G10)



Regression ** Significant at 0.01 probability (t test)

Figure 3. Reducing sugars, and amino acids concentration in leaves of forage sorghum plants of different genotypes, after 60 days of irrigation with saline solutions of different electrical conductivity levels

The BRS-655, BRS-610, 1.016.013 and 1.016.031 genotypes presented the highest chlorophyll a and b contents. The lowest content of this variable was found in the F305 genotype, which had also the lowest photosynthesis. Priori et al. (2003) also found correlation between chlorophyll content and photosynthetic activity. Chlorophyll a and b contents make chlorophyll-protein complexes, which are important for the regulation and organization of photosystems, and essential for production of the chemical energy used in photoassimilate synthesis (Morais et al., 2007).

The salinity levels evaluated did not affect the chlorophyll a and b contents. This may indicate an adaptive mechanism of this species to prevent degradation of these pigments caused by the effect of toxic ions, such as Na⁺ and Cl⁻. Jamil et al. (2007) stated that salinity reduces the chlorophyll content in plants susceptible to salt stress, and increases chlorophyll content in plants tolerant to salt stress. Graciano et al. (2011) found increments in chlorophyll content in peanut leaves with increasing salinity levels, thus increasing photosynthetic efficiency, and attributed this result to a compensatory mechanism of the plant that maintain its growth and production.

Reducing sugars, and amino acids concentration had gradual increases with increasing salinity levels, regardless of the genotype (Figure 3). Leaf soluble sugar concentration also increased linearly, regardless of the genotype; however, the linear regression showed low coefficient of determination ($\hat{y} = 30.0 + 1.17^{**}x$, $R^2 = 0.50$). Changes in total soluble protein concentration were not found under these same conditions.

The comparison between the highest and lowest salinity levels showed increases of 106% for reducing sugars, 67% for soluble sugar, and 129% for amino acids. However, when an absolute increase of these solutes in the leaves was observed, the soluble sugars predominated over the others. Similarly, Lacerda et al. (2001) found high soluble sugar concentrations in forage sorghum genotypes subjected to salinity, which confirms the importance of soluble sugars for the osmotic regulation of leaf cells in this species.

Nonreducing sugars were predominant in the soluble sugar concentration, denoting their probable osmoregulatory function in forage sorghum leaves. Bezerra et al. (2003) reported that the photosynthetic activity is less sensitive to saline stress than the growth, generating an extra production of assimilates, which are not immediately used by the plant and

are accumulated as a compatible solute. Paul & Foyer (2001) stated that the breakdown of starch due to increased amylase activity in the leaf cells results in the release of soluble sugars.

Different from the soluble sugars, the increase in total amino acids concentration with increasing salinity was greater than that of the other organic solutes, however, this increase was not enough to show its capacity of osmoregulation in leaf cells; thus, its function may be linked to the protection of cellular structures (Munns, 2005). The increase in leaf amino acids concentration with increasing salinity levels was also reported by Feijão et al. (2011), who evaluated sorghum-sudangrass, and Lacerda et al. (2001), who studied two forage sorghum genotypes. Moreover, these salinity effects on soluble protein concentration in forage sorghum leaves differed from those found by Sadeghi & Shourijeh (2012), with significant increases with increasing salinity levels.

CONCLUSIONS

1. The photosynthetic activity in forage sorghum plants reduces with increasing salinity, and this response was found in the ten genotypes evaluated.
2. Chlorophyll contents in the leaves of the genotypes evaluated was not affected by the salinity levels used.
3. Concentration of soluble sugars, especially nonreducing sugars, are essential for the osmoregulation in forage sorghum leaves.

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