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Gas exchange and leaf area of banana plants under salt stress inoculated with growth-promoting bacteria[1]

Trocas gasosas e área foliar de bananeiras sob estresse salino inoculadas com bactérias promotoras de crescimento

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HIGHLIGHTS:

Banana cv. Prata Catarina has its gas exchange negatively affected by irrigation water salinity.
Bacillus *sp. did not reduce the harmful effect of salinity on the gas exchange and leaf area of banana.*
Salinity influences the leaf area similarly to photosynthesis.

ABSTRACT: Banana orchards in arid and semiarid regions require the use of irrigation. However, the presence of high concentration of salts in water can impair the development of plants, requiring the evaluation of new technologies to mitigate the effects of stress. The objective of this study was to evaluate gas exchange and leaf area in banana seedlings of the cultivar Prata Catarina inoculated with strains of *Bacillus* spp. under different electrical conductivities of irrigation water. The experiment was carried out in a greenhouse at Embrapa Tropical Agroindustry, Fortaleza, Ceará state, Brazil. The design used was in randomized blocks, in a 4 × 4 factorial scheme, with the first factor being the inoculation treatments: without any application; slow-release fertilizer; Strain 186 and Strain 109, and the second factor being the electrical conductivity of irrigation water (0.5; 1.5; 3.0; 4.5 dS m^{-1}), in five blocks and each plot consisting of three plants. The electrical conductivity of irrigation water negatively influenced the gas exchange of banana cv. Prata Catarina in the vegetative stage, during the 89 days of cultivation. The *Bacillus* spp. strains 186 and 109 did not improve the gas exchange and leaf area of plants under salinity conditions.

Key words: *Bacillus* sp., photosynthetic limitations, growth, salinity

RESUMO: Os pomares de banana em regiões áridas e semiáridas requerem o uso de irrigação. Porém, a presença de altos teores de sais na água pode prejudicar o desenvolvimento das plantas, exigindo a busca de tecnologias para amenizar os efeitos do estresse. O objetivo deste estudo foi avaliar as trocas gasosas e área foliar em mudas de bananeira da cultivar Prata Catarina inoculadas com cepas de *Bacillus* spp. sob diferentes valores de condutividade elétrica da água de irrigação. O experimento foi conduzido em casa de vegetação na Embrapa Agroindústria Tropical, Fortaleza, Ceará, Brasil. O delineamento utilizado foi em blocos casualizados, em esquema fatorial 4 × 4, sendo o primeiro fator os tratamentos de inoculação: sem qualquer aplicação; fertilizante de liberação lenta; as linhagens 186 e 109 e o segundo fator a condutividade elétrica da água de irrigação (0,5; 1,5; 3,0; 4,5 dS m^{-1}), em cinco blocos sendo cada parcela constituída por três plantas. A condutividade elétrica da água de irrigação influenciou negativamente as trocas gasosas da bananeira cv. Prata Catarina na fase vegetativa, aos 89 dias de cultivo. Os *Bacillus* spp. 186 e 109 não melhoraram as trocas gasosas nem aumentaram a área foliar das plantas em condições de salinidade.

Palavras-chave: *Bacillus* sp., limitações fotossintéticas, crescimento, salinidade

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Introduction

The Brazilian Northeast has the largest area cultivated with banana in the country, with 177,300 ha, and the second largest production, with 2.2 million tons (Agrianual, 2019; IBGE, 2020). In 2020, the mean annual banana production in the Southeast and Northeast regions exceeded 2300 million tons for both regions, with 14 thousand fruits produced per hectare in the Southeast region and more than 15 thousand produced per hectare in the Northeast region (IBGE, 2020).

Micropropagation, besides allowing the quality characteristics of the seedling, allows a rapid multiplication and uniformity of production (Singh et al., 2011). However, a possible disadvantage of this technology is the fragility of the seedlings, which require an acclimatization phase. This phase is very sensitive and the use of water with high concentrations of salts, a common condition in the Brazilian Northeast region, can cause varying degrees of stress in plants and reduction of production potential (Larcher, 2004). Thus, it is extremely important to search for production technologies that can enable the use of low-quality waters (Soares et al., 2016). An alternative to attenuate salt stress in plants may be the use of growth-promoting bacteria (PGPB).

The use of bacterial inoculation, in particular PGPB, is effective and environmentally friendly to improve plant stress tolerance. Several studies have already pointed out that the use of these growth-promoting bacteria effectively improves plant growth in the presence of environmental stress conditions imposed on agricultural crops (Bacilio et al., 2004; Mayak et al., 2004; Nabti et al., 2010; Ji et al., 2014; Islam et al., 2015; Majeed et al., 2015; Rolli et al., 2015; Timmusk et al., 2015).

However, there are still few studies associating the attenuation of stress effects with the use of these microorganisms in the banana crop. Knowing that salinity severely affects younger banana plants, the present study aimed to evaluate the use of *Bacillus* sp. strains to reduce the effects of irrigation-water salinity on the gas exchange of seedlings of 'Prata Catarina' banana.

Material and Methods

The study was conducted from April to July 2019 in a screened environment belonging to Embrapa Tropical Agroindustry, Fortaleza, Ceará state, Brazil, with geographic coordinates: 3° 45' South latitude, 38° 33' West longitude and mean altitude of approximately 19 m. During the experimental period, the mean temperature of 27.3 °C and relative air humidity of 77.6% were recorded (Figure 1).

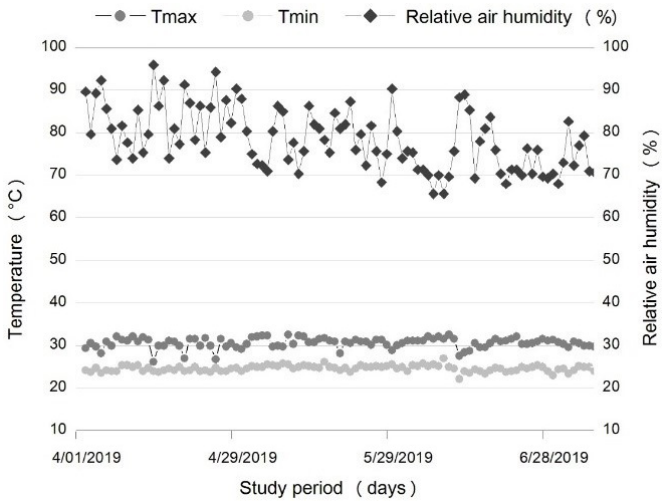


Figure 1. Maximum (Tmax) and minimum (Tmin) temperature and relative air humidity data during the study period

The banana seedlings cv. Prata Catarina (*Musa* sp.) were produced by micropropagation at BioClone Company, Ceará state, Brazil. Seedlings of banana were subjected to a pre-acclimatization period in a room with controlled temperature (28 °C) and artificial light for seven days and later sent to a greenhouse where they were placed under reduced light by adding shade (75%) for seven days. After the pre-acclimatization period, the seedlings were kept under greenhouse conditions with reduced light (50%) for more 30 days.

After that time, the seedlings were transplanted to polyethylene bags containing substrate and both inoculation and salinity treatments started. After 30 days of transplanting, reapplication of the inoculum was performed.

The substrate was composed of a 1:1 proportion of soil and commercial substrate (Table 1), which underwent two autoclaving processes at 121 °C for one hour, under pressure of 1 atm, with an interval of 24 hours. Autoclaving did not alter the chemical characteristics of the soil and substrate, ensuring their sterilization, without preventing the use for cultivation of banana plants.

The design adopted was randomized blocks, in a 4 x 4 factorial scheme. The first factor was the inoculation treatments: without any application; slow-release fertilizer (Osmocote® 14-14-14 at a dose of 5.0 kg m^{-3}); and Strains 186 and 109 (inoculation with *Bacillus* spp.), obtained from the banana rhizosphere, adapted to this host. The isolates were selected because of promising results in promoting growth in experiments with micropropagated banana seedlings (data not yet published). The second factor consisted of electrical

Table 1. Chemical characteristics of the soil and commercial (com.) substrate used in the experiment, before and after the autoclaving process

	pH	EC (dS m^{-1})	Total-N (g kg^{-1})	Ca	Mg	K	Na	P	S	NH_4-N	NO_3-N
				(mg L^{-1})							
Com. substrate	6.0	0.24	15.2	2197	375	27	63	1	1333	11	122
Autoclaved soil	5.7	0.23	15.1	2106	406	48	106	2	1466	47	63
	OM (g kg^{-1})	pH	P (mg dm^{-3})	K	Ca	Mg	Na	H + Al	Al^{+3}	SB	CEC	V (%)
				($mmol_c$ dm^{-3})								
Natural soil	6.2	5.5	9.4	1.2	11	5	0	21.8	0.4	18	39	45
Autoclaved soil	5.7	5.6	5.6	1.3	10	5	0	23.8	0.0	17	41	41

EC - electrical conductivity; OM - organic matter; pH - hydrogen potential; SB - sum of bases; CEC - cation exchange capacity; V - base saturation; Analysis conducted at Soil Laboratory of Embrapa Tropical Agroindustry

conductivities of irrigation water (0.5; 1.5; 3.0; 4.5 dS m^{-1}). The treatments were arranged in five blocks, each plot consisting of three plants.

The two bacterial strains used in the experiment belong to the Collection of Bacteria and Fungi of the Laboratório de Patologia Pós-colheita of Embrapa Agroindústria Tropical, both from research conducted by this laboratory, from the isolation of rhizospheres of banana plants in the brazilian Northeast region, which were free from pathological problems and had good vegetative development in the field, under banana cultivation soil conditions. Strain 186 was collected on April 20, 2016, from the rhizosphere of the banana cultivar Williams, in the municipality of Assu, RN, Brazil. Strain 109 was collected on June 29, 2015, being isolated from the rhizosphere of the banana cultivar Nanica grown in the municipality of Missão Velha, CE, Brazil.

The suspensions of inoculum of the *Bacillus* spp. strains 186 and 109 were prepared by obtaining the biomass: the pre-inoculum, obtained from a portion of activated strains immersed in 50 mL of NYD (dextrose 10 g L^{-1}, yeast extract 5 g L^{-1}, meat extract 3 g L^{-1} and meat peptone 5 g L^{-1}) medium, remained in growth for 24 hours at 30 °C and under rotation of 150 RPM, in a horizontal shaker with temperature control. Subsequently, a 50-µL aliquot of the pre-inoculum was diluted in 100 mL of NYD medium and put back to grow in order to obtain the inoculum. After 24 hours, the bacterial suspension was transferred to Falcon tubes and centrifuged for 10 min at 3500 RPM and 25 °C. This procedure was repeated for two more consecutive times to remove the entire culture medium, and saline solution was used during washes to avoid plasmolysis of bacterial cells. Finally, each bacterial suspension was diluted in 200 mL of saline solution to adjust the concentration to approximately 1.2 x 10^9 CFU mL^{-1}.

The solution with the strains was applied via soil, applying 4.0 x 10^9 CFU mL^{-1} of substrate, with a sterile syringe. The slow-release fertilizer was applied via soil, using the fertilizer Osmocote® 14-14-14 (5.0 kg m^{-3}) (Nomura et al., 2008).

Salinity levels were induced in irrigation water with different electrical conductivities (ECw), following the relationship between ECw and concentration ($mmol_c$ L^{-1} = EC x 10), according to Richards (1954). The solutions with the different concentrations of salts were prepared by adding the salts of sodium chloride, calcium chloride and magnesium chloride, in the equivalent proportion of 7:2:1 (Aquino et al., 2007), and adjusted using a conductivity meter, except for the ECw of 0.5 dS m^{-1}, which corresponded to the salinity of the water from the local water supply.

The electrical conductivity of the soil was measured at 30 days after the second inoculation of the bacterial strains for all saline treatments (60 days after the beginning of irrigation with saline water) (Table 2).

Table 2. Mean electrical conductivity of the soil after bacteria reinoculation after 30 days of irrigation with saline water

Inoculation treatments	Electrical conductivity of irrigation water (dS m^{-1})			
	0.5	1.5	3.0	4.5
Control -	0.74	1.39	2.06	2.43
Control +	0.94	1.93	2.44	3.22
Strain 186	1.11	1.57	2.02	2.53
Strain 109	1.14	1.56	2.15	2.66

The amount of saline water applied daily was calculated by monitoring the weight of the "bag with substrate + plant" set, with the aid of a precision electronic digital scale.

The evaluations of leaf gas exchange were performed at 30, 45 and 60 days after saline water application (DSWA), using an IRGA infrared gas analyzer (ACD, model LCPro SD, Hoddesdon, UK) with air flow of 300 mL min^{-1} and 1200 µmol m^{-2} s^{-1} coupled light source. Measurements of stomatal conductance (gs, mol m^{-2} s^{-1}), transpiration rate (E, mol m^{-2} s^{-1}), net CO_2 assimilation rate (A, µmol m^{-2} s^{-1}) the internal concentration of CO_2 (Ci, ppm), instantaneous water use efficiency (A/gs) calculated by relating it to net photosynthesis with stomatal conductance [(µmol m^{-2} s^{-1}) (mol m^{-2} s^{-1})$^{-1}$] and the instantaneous efficiency of carboxylation (A/Ci) [(µmol m^{-2} s^{-1}) (µmol m^{-2} s^{-1})$^{-1}$] of the relationship between net photosynthesis and internal concentration of carbon were always taken from 8 to 12 a.m.

Leaf area (cm^2) was measured at 60 days after saline water application using a leaf area meter (LI - 3100, Area Meter, Li-Cor., Inc., Lincoln, 87 Nebraska, USA).

The assumptions of ANOVA were verified and, with the data considered normal, the results were subjected to analysis of variance and regression analysis. When the inoculation treatments showed a significant difference, their means were compared by Tukey test using the Sisvar® statistical software (Ferreira, 2011). The analysis was carried out separately for each evaluation period.

Results and Discussion

Bacterial treatments had a significant effect on the plants' net CO_2 assimilation rate and instantaneous carboxylation efficiency (A/Ci) only at 30 and 45 DSWA, while transpiration was affected at 45 DSWA, with no effect on stomatal conductance and with alteration of the internal CO_2 concentration at 30 and 60 DSWA. The instantaneous water use efficiency (A/gs) only showed a statistical difference at 60 DSWA (Table 3).

Electrical conductivity of irrigation water impacted CO_2 assimilation rate, stomatal conductance, transpiration and Ci at 30 DSWA, CO_2 assimilation rate, transpiration and A/Ci at 45 DSWA, and Ci and A/gs at 60 DSWA (Table 3). There was also interaction between the factors for CO_2 assimilation rate at 45 and for Ci at 60 DSWA (Table 3).

The analysis of variance shows significant effect of the blocks, due to the spatial orientation of the greenhouse throughout the day, where the intensity of the radiation reaching the plants varied in the various quadrants of the environment. Therefore, the high coefficients of variation observed for the variables analyzed were due to the nature of these variables and the heterogeneity among the plants.

At 30 and 45 DSWA, the CO_2 assimilation rates (A) of plants were affected by the inoculated treatments. At 60 DSWA, there was no statistically significant effect for bacterial treatments. In both evaluations, the control + had the highest values of A (Figures 2A and B).

Transpiration only showed a difference at 45 and 60 DSWA. At 45 days of saline irrigation the control - and control + showed higher values of E, while at 60 DSWA the control +

Table 3. Summary of analysis of variance for CO_2 assimilation rate (A), stomatal conductance (gs), transpiration (E), internal CO_2 concentration (Ci), instantaneous water use efficiency (A/gs) and instantaneous carboxylation efficiency (A/Ci) of banana plants cv. Prata Catarina at 30, 45 and 60 days after irrigation with saline water (DSWA)

Sources of variation	DF	Mean squares					
		A	gs	E	C_i	A/gs	A/Ci
				30 DSWA			
Block	4	12.112^{ns}	0.32^{ns}	10.347**	1478.937**	404.334**	0.0001^{ns}
Growth-promoting treatment	3	34.156*	0.25^{ns}	0.0210^{ns}	742.612**	39.919^{ns}	0.0004*
Salinity	3	43.326*	0.71*	1.360*	97.912^{ns}	160.841^{ns}	0.0001 *
Growth-promoting treatment x Salinity	9	11.211^{ns}	0.12^{ns}	1.665^{ns}	174.379^{ns}	71.976 ^{ns}	0.0001^{ns}
Residual	60	11.307	0.18	0.347	198.690	91.771	0.00^{ns}
CV (%)	-	28.56	45.28	21.26	4.53	53.05	30.49
				45 DSWA			
Block	3	9.078^{ns}	0.266*	1.757**	5219.083^{ns}	4195.649**	0.0001^{ns}
Growth-promoting treatment	3	67.5768*	0.165^{ns}	0.669*	3541.750^{ns}	1503.693^{ns}	0.0001**
Salinity	3	50.994**	0.330^{ns}	0.843**	4620.885^{ns}	2451.288*	0.0008**
Growth-promoting treatment x Salinity	9	16.517*	0.077^{ns}	0.516^{ns}	1626.958^{ns}	481.605^{ns}	0.0001^{ns}
Residual	45	7.444	0.071	0.23	1865.783	431.616	0.0001
CV (%)	-	23.79	46.95	34.5	15.22	64.77	29.98
				60 DSWA			
Block	3	15.32^{ns}	0.15^{ns}	7.03**	2773.31**	462.377**	0.0008**
Growth-promoting treatment	3	7.93^{ns}	0.29^{ns}	2.83^{ns}	1247.81**	484.468**	0.000^{ns}
Salinity	3	14.14^{ns}	0.77**	2.77^{ns}	1534.18**	0688.746**	0.0002^{ns}
Growth-promoting treatment x Salinity	9	5.83^{ns}	0.15^{ns}	0.48^{ns}	634.83**	170.526^{ns}	0.0001^{ns}
Residual	45	8.23	0.11	1.15	295.62	97.916	0.0001
CV (%)	-	33.76	44.90	29.06	4.58	48.08	34.87

DF - Degrees of freedom; CV - Coefficient of variation; **; * and ^{ns} - Significant at $p \leq 0.01$ and $p \leq 0.05$ and not significant by the F test, respectively

showed a lower value of transpiration (Figures 2C and D). The stomatal conductance was not affected by inoculation treatments in any of the evaluated periods.

In general, the internal concentration of CO_2 (Ci) was lower in plants that received fertilization, with no difference between the other treatments (Figures 2E and F).

The results show little effect of the growth-promotion treatments on gas exchange at this stage of development of banana seedlings.

A high rate of photosynthesis in most cases is due to the increase in stomatal conductance, which allows for greater absorption and consequent fixation of CO_2 (Taiz et al., 2017), which is not observed in the present study. Thus, the higher photosynthetic rate in plants that received fertilization is associated with the higher carboxylation efficiency of ribulose 1,5 bisphosphate (RuBP) carboxylase/oxygenase (RuBisCO) (Figures 2G and H). Leaf photosynthesis according to Gago et al. (2020) is totally dependent on the availability of CO_2 at the carboxylation sites and, therefore, is strongly influenced by gs.

According to Makino (2011) and Warren & Adams (2001), the deficiency of N mainly in the leaves directly reduces the activity and the content of RuBisCO, which in turn affects photosynthesis, which may have happened in the other treatments.

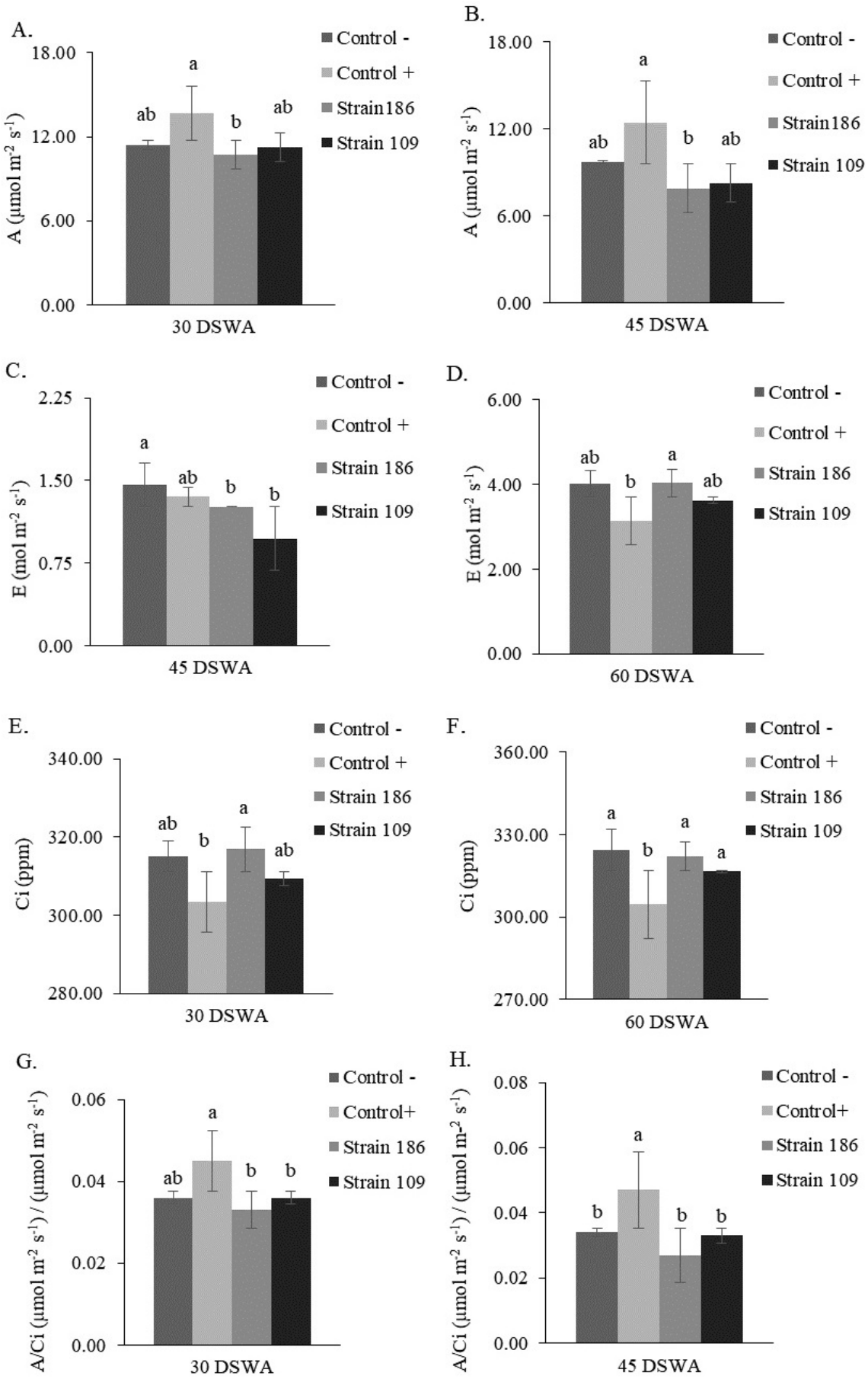
In addition, it is observed that the treatment with a higher photosynthetic rate (Control +) promoted a reduction in the internal concentration of CO_2 (Figures 2E and F), but still at a concentration that is not restrictive to the photosynthetic process, as a result of maintaining the stomatal opening and carboxylation efficiency. The lower Ci can cause changes in the activity of the carboxylase enzyme RuBisCO for oxygenase, that is an increase in photorespiration and a decrease in net CO_2 assimilation rate (Marenco et al., 2014).

Arantes (2014), evaluating vegetative and physiological characteristics of six cultivars of Prata banana in a semi-arid environment, reported that the values of stomatal conductance (gs) were around 1.0 mol H_2O m^{-2} s^{-1}, observed at 8 a.m., with the lowest value (0.12 mol H_2O m^{-2} s^{-1}) observed at 14 p.m., values that were above those found in the present study, which averaged 0.94 mol m^{-2} s^{-1} at 30 DSWA, 0.57 mol m^{-2} s^{-1} at 45 DSWA and 0.75 mol m^{-2} s^{-1} at 60 DSWA.

Although the main function of the bacteria used in this study is to promote plant growth, the leaf area was larger in plants that received mineral fertilization (Figure 3), showing that CO_2 fixation was the main factor for leaf growth. The high concentration of CO_2, according to Kant et al. (2012) and Morales et al. (2018), commonly leads to the stimulation of photosynthesis and the growth potential of C3 plants. In this context, ample evidence, obtained in experiments conducted in controlled environmental chambers, shows that the negative effects of salinity on plant growth can be mitigated by an increase in CO_2 (Brito et al., 2020).

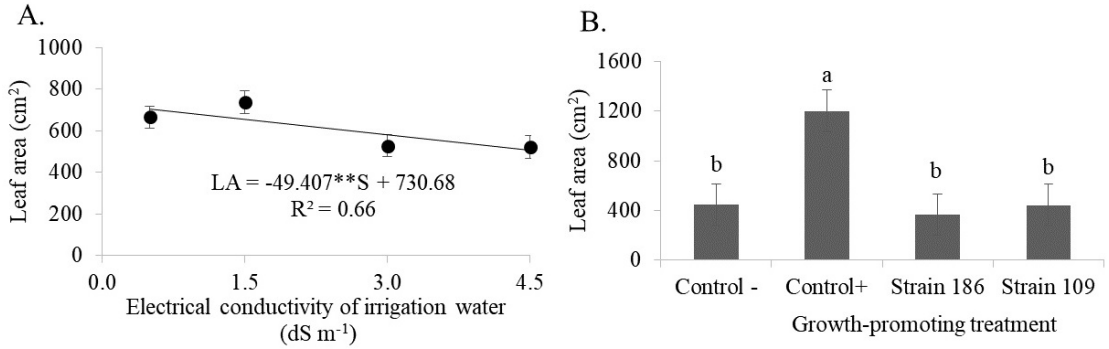
With respect to saline treatments, for the net CO_2 assimilation rate, a significant effect was observed, which led to a linear fit with decreasing values of A at 30 and 45 DSWA, with maximum values of 14.01 and 12.21 µmol m^{-2} s^{-1}, respectively (Figure 4A). At 60 DSWA, there were no relevant changes in CO_2 assimilation rate, which can be explained by the climatic conditions at the end of the experiment, especially the presence of many clouds, reducing photosynthetically active radiation, which is confirmed by the occurrence of a lower mean photosynthetic rate in that period (9.08 µmol m^{-2} s^{-1}). Plants may also have acclimated to salt stress, as observed by Siva et al. (2014) and Santana Junior et al. (2020).

For some authors, the reduction in stomatal conductance is a mechanism of salinity tolerance, which reduces water losses through the stomata and minimizes the occurrence of desiccation of the plant, thus favoring its development even under adverse conditions (Silva et al., 2014). This tolerance mechanism, however,



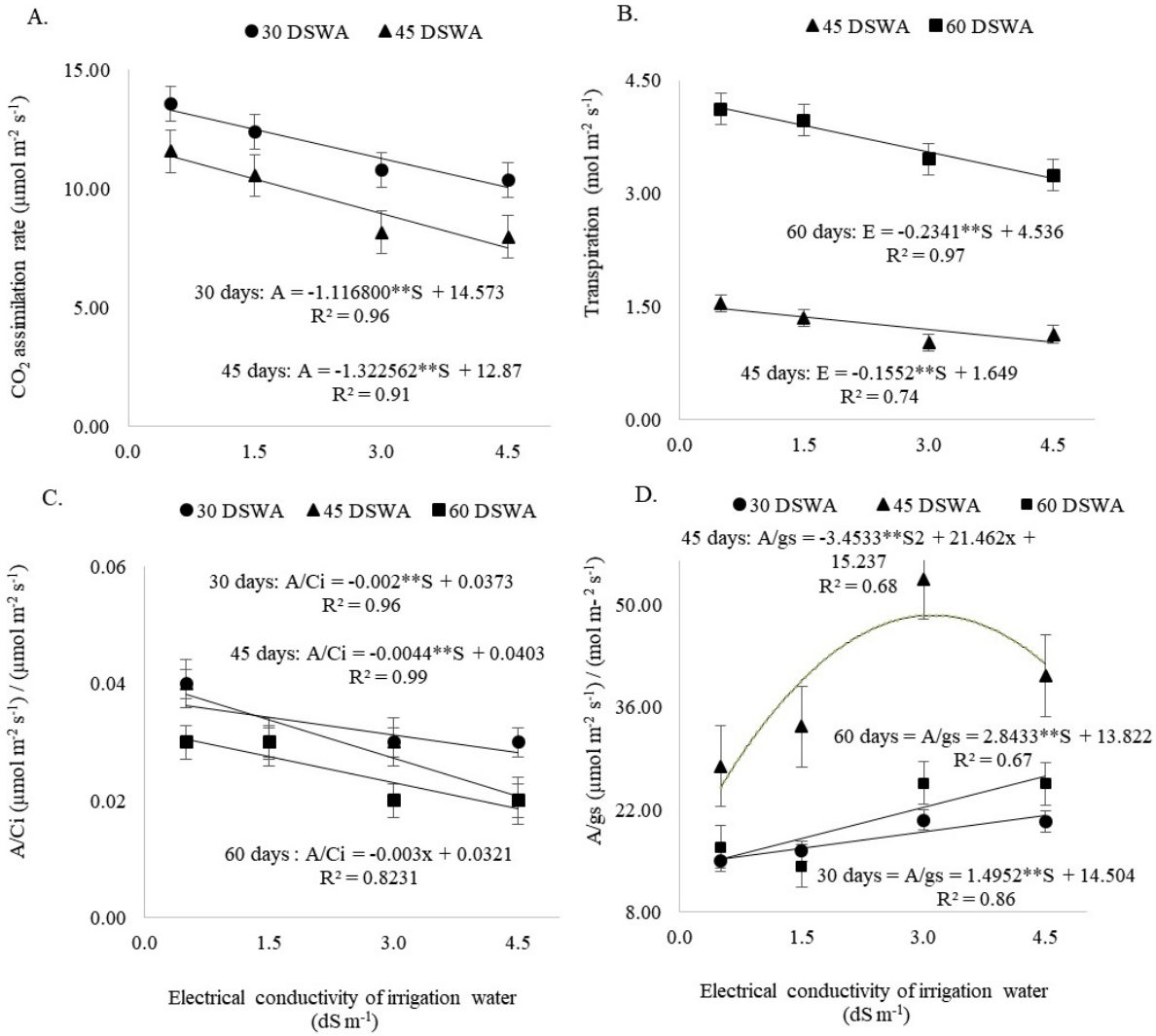
Control -: No application of fertilizers or bacteria; control +: application of slow-release fertilizer; Strain 186 (*Bacillus* sp.); Strain 109 (*Bacillus* sp.); CO_2 assimilation rate (A and B), transpiration (C and D), internal CO_2 concentration (E and F) and instantaneous carboxylation efficiency (G and H) of banana cv. Prata Catarina. Means followed by the same lowercase letters do not differ statistically from each other at $p \leq 0.05$ by the Tukey test. Vertical lines represent standard error (n = 4)

Figure 2. Physiological variables of banana plants inoculated with *Bacillus* spp. at 30, 45, and 60 days after irrigation with saline water (DSWA)



Control -: No application of fertilizers or bacteria; control +: application of slow-release fertilizer; Strain 186 (*Bacillus* sp.); Strain 109 (*Bacillus* sp.); Means followed by the same lowercase letters do not differ statistically from each other at p ≤ 0.05 by the Tukey test. ns - Not significant and ** - Significant at p ≤ 0.01 by F test. Vertical lines represent standard error (n = 4)

Figure 3. (A): Leaf area of banana cv. Prata Catarina as a function of electrical conductivity of irrigation water and (B) leaf area of banana plants inoculated with *Bacillus* spp. and irrigated with saline water at 60 days after irrigation with saline water



ns - Not significant and ** - Significant at p ≤ 0.01 by F test. Vertical lines represent standard error (n = 4)

Figure 4. CO_2 assimilation rate (A), transpiration (B), instantaneous carboxylation efficiency (A/Ci) (C) and instantaneous water use efficiency (A/gs) (D) of banana cv. Prata Catarina as a function of electrical conductivity of irrigation water at 30, 45 and 60 days of irrigation with saline water (DSWA)

reduces plant growth and yield. In present study, no significant regression was found for stomatal conductance and Ci.

The non-significant effect for stomatal conductance suggests that the reduction in photosynthesis as a function of salinity was due to other factors. The 28% reduction in leaf area as salinity increased from lowest to the highest level of salinity (Figure 3A) may have influenced a reduction by photosynthesis feedback, due to the decrease in the need for the production of photoassimilates (Galmés et al., 2007; Flexas et al., 2009; Gago et al., 2020). On the other hand, there was a reduction in carboxylation efficiency at 30 and 45 days after saline treatment (Figure 4C), which also suggests that RuBisCO (ribulose-1,5-

bisphosphate carboxylase oxygenase) may have been affected by salinity (Makino et al., 2011).

A significant effect was observed according to the linear regression model for the transpiration (E) at 45 and 60 DSWA, showing a reduction in the transpiratory rate of the plants as the salt level increased. The maximum value of E at 45 DSWA was 1.57 mol m^{-2} s^{-1} and at 60 DSWA it was 4.13 mol m^{-2} s^{-1}. The reduction in E from the lowest to the highest salt concentration at 45 DSWA was 39.51%, while at 60 DSWA the reduction was 22.52% (Figure 4B).

Similar to the results found in the present study at 60 DSWA, Santana Junior et al. (2020), evaluating the effect of irrigation water salinity levels during the vegetative stage in banana cultivars, observed a reduction in transpiration with the increase in irrigation water salinity.

The reduction in transpiration was less marked than that of photosynthesis, which can be seen by the increase in A/gs at 30 and 60 DSWA after the imposition of saline treatments (Figure 4D).

Conclusions

1. The electrical conductivity of irrigation water negatively influenced the gas exchange of banana cv. Prata Catarina in the vegetative stage, during the 89 days of cultivation.

2. The use of *Bacillus* spp. strains 186 and 109 did not promote improvements in the gas exchange of banana plants subjected to salt stress conditions.

3. Photosynthesis and leaf area showed similar behavior as a function of increased salt stress.

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