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Foliar application of proline on the mitigation of salt stress in the physiological indices of sour passion fruit

Aplicação foliar de prolina na mitigação do estrese salino nos índices fisiológicos de maracujazeiro-azedo

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Highlights

Sour passion fruit is moderately sensitive to salt stress in the seedling phase.
High salt concentrations in irrigation water impair seedling production.
Foliar application of proline does not minimize the deleterious effects of salinity.

Abstract

Salinity is one of the main abiotic stresses that significantly constrict plant growth and lead to substantial reductions in crop yield. The adverse effects of salt stress are particularly pronounced in semi-arid regions, due to unfavorable climatic conditions and the presence of high-salinity water sources. In this context, the exploration of strategies for utilizing saline water in irrigation is essential to address the global food production demand. Therefore, the objective of this study was to assess the impact of foliar application of proline concentrations on the physiological indices of sour passion fruit during the seedling formation phase, with saline water as the irrigation source. The research was carried out within a greenhouse belonging to the Agricultural Engineering Academic Unit of the Federal University of Campina Grande,

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situated in Campina Grande – PB, Brazil. The study employed a completely randomized experimental design, organized in a 5 × 4 factorial arrangement consisting of five levels of electrical conductivity in the irrigation water (ECw: 0.6, 1.2, 1.8, 2.4, and 3.0 dS m^{-1}) and four concentrations of proline (0, 5, 10, and 15 mM). Each treatment combination was replicated four times, and each experimental plot consisted of two sour passion fruit plants, resulting in a total of 160 experimental units. Irrigation with water having an electrical conductivity of 0.6 dS m^{-1} induced a reduction in relative water content and gas exchange and increased electrolyte leakage in the leaf blade of sour passion fruit plants. Irrigation with water exhibiting an electrical conductivity within the range of 1.3 to 1.8 dS m^{-1} stimulated the biosynthesis of photosynthetic pigments in the sour passion fruit cultivar 'BRS GA1', as observed 66 days after sowing. Foliar application of proline at concentrations ranging between 4.5 and 6.5 mM resulted in increased stomatal conductance, transpiration rates, CO_2 assimilation rates, instantaneous carboxylation efficiency, and chlorophyll content of sour passion fruit plants.

Key words: *Passiflora edulis* Sims. Salinity. Osmolyte synthesis.

Resumo

A salinidade é um dos principais estresses abióticos que restringe o crescimento das plantas e causa perdas significativas no rendimento. Os efeitos do estresse salino são mais severos em regiões semiáridas, devido as condições climáticas e a ocorrência de fontes hídricas com teores elevados de sais. Neste contexto, a busca por estratégias que viabilizem o uso de águas salinas na irrigação é fundamental para garantir a necessidade de produção de alimentos. Assim, objetivou-se com este estudo avaliar os efeitos das aplicações foliar de concentrações de prolina nos índices fisiológicos de maracujazeiro-azedo irrigados com águas salinas na fase de formação de mudas. A pesquisa foi conduzida em casa de vegetação pertencente à Unidade Acadêmica de Engenharia Agrícola da Universidade Federal de Campina Grande, em Campina Grande – PB, utilizando-se o delineamento experimental inteiramente casualizado, em esquema fatorial 5 × 4, sendo cinco níveis de condutividade elétrica da água de irrigação CEa - (0,6; 1,2; 1,8; 2,4 e 3,0 dS m^{-1}) e quatro concentrações de prolina (0, 5, 10 e 15 mM) com quatro repetições e cada parcela continha duas plantas, totalizando 160 unidades experimentais. A salinidade da água a partir de 0,6 dS m^{-1} reduziu o conteúdo relativo de água, trocas gasosas, e elevou o extravasamento de eletrólitos no limbo foliar das plantas de maracujazeiro-azedo. A irrigação com água de condutividade elétrica entre 1,3 e 1,8 dS m^{-1} estimulou a biossíntese de pigmentos fotossintéticos do maracujazeiro-azedo 'BRS GA1', aos 66 dias após a semeadura. A aplicação foliar de prolina nas concentrações variando de 4,5 e 6,5 mM aumentou a condutância estomática, a transpiração, a taxa de assimilação de CO_2, a eficiência instantânea de carboxilação e os teores de clorofilas do maracujazeiro-azedo.

Palavras-chave: *Passiflora edulis* Sims. Salinidade. Síntese de osmólitos.

Introduction

Excess salt in water and/or soil leads to salt stress, one of the main abiotic factors constraining agricultural production and economic viability and favoring soil degradation (Soares et al., 2018; Silva et al., 2019). Climate changes seen in recent years, such as rising temperatures, reduced precipitation, increased sunlight, and global warming, exacerbate the impact of salinity, particularly in semi-arid regions (Dias et al., 2018; Seleiman et al., 2021; Lima et al., 2020a). Concurrently, the combination of limited water resources for use in agriculture and changing climate patterns has driven the increased use of saline water for irrigation (Lima et al., 2018; González-Delgado et al., 2023).

Salt stress diminishes a plant's capacity to absorb water and essential nutrients, leading to the generation of harmful reactive oxygen species (ROS). These, in turn, damage photosynthetic pigments, reduce relative water content, and hinder gas exchange in leaves, directly affecting crop growth and development (Lima et al., 2020b; Anwar et al., 2023).

Therefore, it is crucial to explore strategies that enable the use of saline water in agriculture, particularly in regions where the availability of fresh water for agricultural purposes constitutes a challenge. One promising strategy is the foliar application of proline, a low-molecular-weight cyclic amino acid known as a key osmoprotectant. Experimental evidence has shown that proline can enhance salinity tolerance in plants, preserving cell membrane integrity and stabilizing enzymes/proteins (Zhu et al., 2020; Torres et al., 2023).

Sour passion fruit (*Passiflora edulis* Sims) is a crop highly sensitive to salt stress, with a critical threshold for irrigation water salinity set at 1.3 dS m^{-1} (Galvão Sobrinho et al., 2023). Brazil, being the world's leading producer and consumer of passion fruit, recorded a production of 697,859 t in 2022, cultivated across 45,602 ha, making an average yield of 15,303 t ha^{-1}. The northeast region of the country contributed significantly to national production, accounting for 69.77% (496,893 t), with key production in the states of Bahia (227,867 t), Ceará (148,013 t), and Pernambuco (37,160 t) (Instituto Brasileiro de Geografia e Estatística [IBGE], 2022).

This study examines the hypothesis that foliar application of proline, at appropriate concentrations, can alleviate the detrimental effects of saline water irrigation on the physiological indices of sour passion fruit. This is expected to enhance the plant's ability to tolerate salt stress, improve gas exchange, promote the biosynthesis of photosynthetic pigments, and reduce electrolyte leakage from the leaf blade through the activity of ROS-detoxifying enzymes. To achieve these objectives, the study evaluates the effect of various concentrations of foliar-applied proline on the physiological indices of sour passion fruit during the seedling formation phase when subjected to saline water irrigation.

Material and Methods

The experiment was conducted from July to October 2022 in a greenhouse situated within the Agricultural Engineering Academic Unit – UAEA, at the Federal University of Campina Grande - UFCG, located in Campina Grande - PB, Brazil (7º15'18" S, 35º52'28" W; 550 m above sea level). The region's climate is classified as tropical AS, characterized by a dry season (Alvares et al., 2013). Figure 1 displays the temperature (both maximum and minimum) and relative humidity data recorded within the greenhouse.

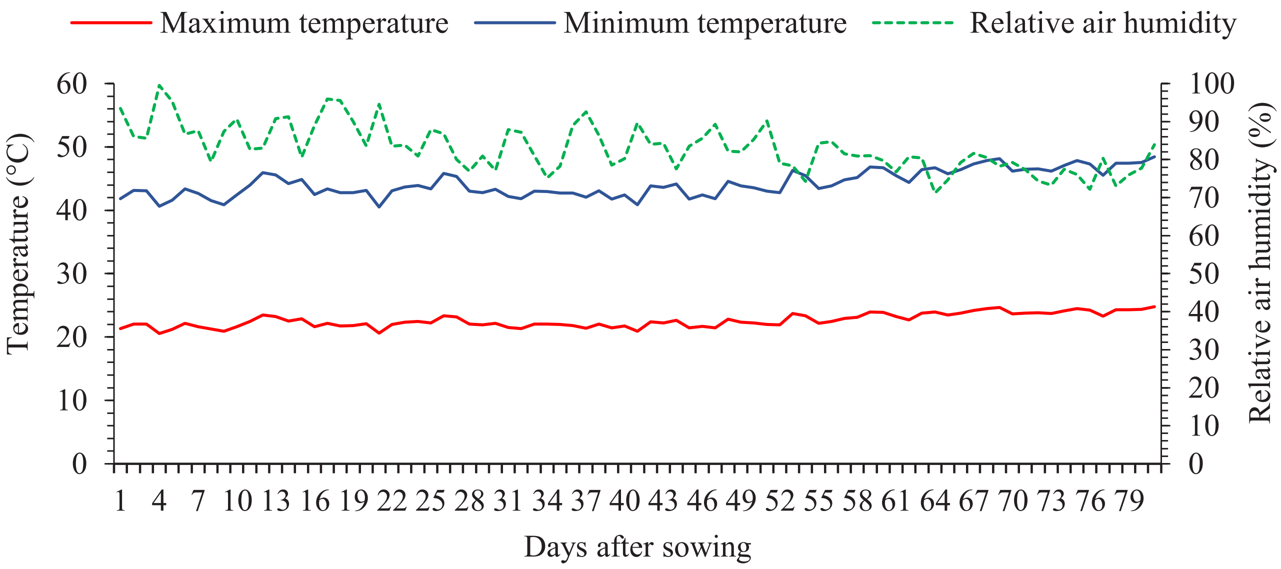

Figure 1. Maximum and minimum temperature data and relative humidity during the experiment period.

The experimental treatments comprised five levels of electrical conductivity in the irrigation water (0.6, 1.2, 1.8, 2.4, and 3.0 dS m^{-1}) and four proline concentrations (0, 5, 10, and 15 mM). These treatments were arranged in a 5 × 4 factorial design and were distributed using a completely randomized design, with each treatment replicated four times. Each experimental plot consisted of two plants, resulting in a total of 160 experimental units. The selection of these salinity levels was based on a study conducted by Ramos et al. (2022) involving sour passion fruit (*Passiflora edulis* Sims), while the proline concentrations were determined in accordance with research conducted by Veloso et al. (2018) involving the guava crop (*Psidium guajava*) during the seedling formation phase.

This study used cultivar ‘BRS Gigante Amarelo’ (BRS GA1), chosen for its high yield, tolerance to anthracnose and bacteriosis, yellow fruit color, yellowish pulp, pulp yield of 40%, and sugar content of around 15° Brix (Brito et al., 2022).

Sour passion fruit seedlings were propagated via seeds, employing the ‘BRS GA1’ cultivar. The sowing process involved placing three seeds in each polyethylene bag measuring 10 × 25 cm, with a 3-kg capacity. The seeds were evenly distributed at a depth of 1 cm and were sown in a substrate composed of soil from a Regolithic Neosol (Entisol - Psamments) with sandy loam texture, sand, and earthworm humus, in a 2:1:1 ratio by volume. At 37 days after sowing (DAS), thinning was conducted, retaining the most morphologically vigorous plant (one) in each bag. The soil used was collected from a depth of 0-20 cm in an area within the municipality of Lagoa Seca - PB. The physical and chemical properties of the soil (Table 1) and were assessed following the methodology by Teixeira et al. (2017).

Table 1

Chemical and physical characteristics of the soil used in the experiment before implementing the treatments

Chemical characteristics								
pH H_2O (1:2.5)	OM dag kg^{-1}	P (mg kg^{-1})	K^+	Na^+	Ca^{2+}	Mg^{2+}	Al^{3+}	H^+
			....cmol$_c$ kg^{-1}					
6.7	12.75	5.96	89.51	0.09	3.72	0.95	0.00	0.91
..........Chemical characteristics...........				..........................Physical characteristics..........................				
ECse (dS m^{-1})	CEC cmol$_c$ kg^{-1}	SAR (mmol L^{-1})$^{0.5}$	ESP %	Particle fraction (g kg^{-1})			Moisture (dag kg^{-1})	
				Sand	Silt	Clay	33.42 kPa^1	1519.5 kPa^2
0.50	5.89	0.70	1.52	727	211	62	Sandy loam	

pH – potential of hydrogen; OM – organic matter, Walkley-Black wet digestion; Ca^{2+} and Mg^{2+} extracted with 1M KCl, pH 7.0; Na^+ and K^+ extracted using 1M NH_4OAc, pH 7.0; Al_3^{+}+H^+ extracted using 0.5 M CaOAc, pH 7.0; ECse – electrical conductivity of the saturation extract; CEC – cation-exchange capacity; SAR – sodium adsorption ratio of the saturation extract; ESP – exchangeable sodium percentage; ^{1,2} corresponds to field capacity and permanent wilting point.

The waters were prepared by dissolving NaCl, $CaCl_2.2H_2O$, and $MgCl_2.6H_2O$ in a 7:2:1 ratio, mirroring the typical composition of water sources utilized for irrigation in the northeast region (Medeiros, 1992). These solutions adhered to pre-established protocols, with the initial source being the local supply system (Campina Grande - PB). In preparing the irrigation waters, we considered the ratio between ECw and the salt content (Richards, 1954), as according to Eq. 1:

$$A \approx 640 \times ECw \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1),$$

where A = sum of cations (mg L^{-1}); ECw = water electrical conductivity (dS m^{-1}).

After preparing the water with different salinity levels, ECw was checked and adjusted before each irrigation event if necessary.

Before sowing, the soil moisture content was increased to match field capacity using low-salinity water (0.6 dS m^{-1}). Subsequent irrigations occurred daily at 17h00, with the volume tailored to maintain soil moisture close to field capacity in each experimental bag. After 27 DAS, irrigation began with water from the different treatments. The volume of water to be applied followed plant water requirements determined through a water balance equation, as represented by Eq. 2:

$$VI = \frac{(Vp-Vd)}{(1-LF)} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2),$$

where VI = volume of water to be applied in the subsequent irrigation event (mL); Vp = volume applied in the previous irrigation event (mL); Vd = volume drained (mL); and LF = leaching fraction of 0.20 (aimed at reducing the gradual accumulation of salts in the soil).

Nitrogen, potassium, and phosphorus fertilization was conducted in accordance with the guidelines provided by Novais et al. (1991), using urea, potassium chloride, and monoammonium phosphate to apply 100, 150, and 300 mg kg^{-1} of N, K_2O, and

P_2O_5, respectively. Fertilization was divided into eight installments and carried out at 24, 31, 38, 45, 52, 59, 66, and 73 DAS through fertigation. As a source of micronutrients, Dripsol Micro® (1.2% magnesium, 0.85% boron, 3.4% iron, 4.2% zinc, 3.2% manganese, 0.5% copper, and 0.06% molybdenum) was applied at a concentration of 1 g L^{-1} through foliar application, repeated at seven-day intervals.

Proline concentrations were prepared for each application event by diluting proline in distilled water. Weekly applications were carried out to ensure complete leaf wetting (abaxial and adaxial faces). A manual sprayer with an adjustable 1-cm conical metal nozzle was used, operating at a pressure of 300 Psi and a flow rate of 1.1 L min^{-1}, along with an adjuvant to enhance application efficiency. To prevent drift between experimental plots, a cardboard box was employed. Plants subjected to the concentration of 0 mM were sprayed with distilled water only. All applications were carried out from 17h00 due to the lower temperature. During the seedling formation period, an average spray mixture volume of 200 mL per plant was administered.

Pest control involved the use of a synthetic pyrethroid insecticide with Deltamethrin as the active ingredient. Weeds were manually removed throughout the experiment to prevent interspecific competition for water and nutrients, favoring the full development of the crop.

The effects of treatments on the passion fruit plants were assessed at 66 DAS. Parameters included relative water content (RWC), electrolyte leakage (EL, %), gas exchange (stomatal conductance - *gs*, transpiration - *E*, intercellular CO_2 concentration - Ci, and CO_2 assimilation rate - *A*), instantaneous carboxylation efficiency (*iCE*), instantaneous water use efficiency (*iWUE*), and photosynthetic pigment synthesis (chlorophyll a - *Cl a*, chlorophyll b - *Cl b*, total chlorophyll - *Cl t*, and carotenoids).

To determine the relative water content, five leaf discs were collected from the upper third of each plant. The leaf discs were immediately weighed, avoiding moisture loss, to determine fresh weight (FW). These samples were then placed in plastic bags, immersed in distilled water, and stored for 24 h. After this period, excess water was removed with a paper towel, and the turgid weight (TW) of the samples was determined. The samples were then dried in an oven (temperature ≈ 65 ± 3 °C) until a constant weight was achieved to determine the dry matter (DM). Relative water content was calculated as proposed by Weatherley (1950), as expressed in Eq. 3:

$$\mathrm{RWC} = \frac{(\mathrm{FW} - \mathrm{DM})}{(\mathrm{TW} - \mathrm{DM})} \times 100 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots.(3),$$

where RWC = relative water content (%); FW = leaf fresh weight (g); TW = turgid weight (g); and DM = dry matter (g).

To quantify electrolyte leakage in the leaf blade, five leaf discs were collected from the third fully expanded leaf and subsequently inserted into an Erlenmeyer® flask containing 50 mL of distilled water, sealed with aluminum foil. After 24 h at 25 °C, the initial electrical conductivity (ECi) was measured. The samples were then subjected to a temperature of 90 °C for 120 min in a forced-air oven (SL100/336, SOLAB®). After cooling, the final electrical conductivity (ECf) was measured using a conductivity meter (MB11, MS Techonopon®).

Electrolyte leakage was determined using the method of Scotti-Campos et al. (2013), as shown in Eq. 4:

$$\%\ \mathrm{EL} = \frac{\mathrm{Ci}}{\mathrm{Cf}}\ x\ 100 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots..(4),$$

where % EE = electrolyte leakage (%); Ci = initial electrical conductivity (dS m^{-1}); and Cf = final electrical conductivity (dS m^{-1}).

To quantify the levels of chlorophyll a, b, total, and carotenoids, leaf discs with an area of 1.54 cm^2 were collected from the third fully expanded leaf near the apical bud, following the method suggested by Arnon (1949). Pigment extracts were prepared using 7 mL of acetone diluted to 80%. Using a spectrophotometer, photosynthetic pigment levels were measured at absorbance wavelengths of 470, 647, and 663 nm. Pigment contents were determined using Eqs. 5, 6, 7, and 8.

$$\mathrm{Cl}\ a = (12.21 \times \mathrm{ABS}_{663}) - (2.81 \times \mathrm{ABS}_{647}) \ldots\ldots..(5)$$

$$\mathrm{Cl}\ b = (20.13 \times \mathrm{ABS}_{647}) - (5.03 \times \mathrm{ABS}_{663}) \ldots\ldots\ldots (6)$$

$$\mathrm{Cl}\ t = (7.15 \times \mathrm{ABS}_{663}) + (18.71 \times \mathrm{ABS}_{647}) \ldots\ldots\ldots (7)$$

$$\mathrm{Car} = [(1000 \times \mathrm{ABS}_{470}) - (1.82 \times \mathrm{Cl}\ a) - (85.02 \times \mathrm{Cl}\ b)/198] .. (8),$$

where Cl *a* = chlorophyll a (μg mL^{-1}); Cl *b* = chlorophyll b (μg mL^{-1}); Cl *t* = total chlorophyll (μg mL^{-1}); and Car = carotenoids (μg mL^{-1}).

Gas exchange measurements were conducted at 66 days after sowing (DAS) by employing a portable infrared gas analyzer (LCPro+, ADC BioScientific Ltd.). These measurements were taken on the third fully expanded leaf, counted from the apical bud. Parameters assessed included the CO_2 assimilation rate (*A*, μmol CO_2 m^{-2} s^{-1}), transpiration (*E*, mmol H_2O m^{-2} s^{-1}), stomatal conductance (*gs*, mol H_2O m^{-2} s^{-1}), and intercellular CO_2 concentration (*Ci,* μmol CO_2 m^{-2} s^{-1}). From this dataset, instantaneous water use efficiency (*iWUE* = [(μmol CO_2 m^{-2} s^{-1}) (mmol H_2O m^{-2} s^{-1}) $^{-1}$] and instantaneous carboxylation efficiency (*iCE* = [(μmol m^{-2} s^{-1}) (μmol mo^{l-1}) $^{-1}$]) were computed. The measurements were conducted between 07h00 and 10h00, under natural temperature and CO_2 concentration conditions, utilizing an artificial radiation source delivering 1,200 μmol m^{-2} s^{-1}, which was determined by establishing the photosynthetic light saturation point following the photosynthetic response curve to light (Fernandes et al., 2021).

The collected data were subjected to a normality test (Shapiro-Wilk test) at a significance level of 0.05. Following this, the data underwent analysis of variance utilizing the F test at the significance levels of 0.05 and 0.01. When statistical significance was observed, linear and quadratic polynomial regression analyses were performed using SISVAR statistical software Version 5.6 (Ferreira, 2019). In cases where a significant interaction effect was noted, response surface graphs were generated using SigmaPlot software version 12.5.

Results and Discussion

Water salinity levels had a significant impact on the relative water content (RWC) and electrolyte leakage (EL) of sour passion fruit plants (Table 2). Proline concentrations also had a significant influence on EL in the leaf blade of these plants at 66 DAS. However, the interaction between the factors (SL × PRO) did not show a significant effect on any of the measured variables.

Table 2

Summary of analysis of variance regarding relative water content (RWC) and electrolyte leakage (EL) in the leaf blade of sour passion fruit plants grown under water salinity and proline concentrations, 66 days after sowing (DAS)

Source of variation	DF	Mean square	
		RWC	EL
Salt level (SL)	4	190.07**	212.16**
Linear regression	1	743.34**	740.33**
Quadratic regression	1	1.48ns	39.00ns
Proline concentration (PRO)	3	39.05ns	125.69**
Linear regression	1	13.00ns	229.37**
Quadratic regression	1	89.37*	66.17*
Interaction (SL × PRO)	12	5.58ns	23.28ns
Residual	60	10.21	12.80
CV (%)		4.17	13.76

DF - degrees of freedom; CV - coefficient of variation; (*) significant at $p \leq 0.05$; (**) significant at $p \leq 0.01$ probability; (ns) not significant.

Water salinity linearly decreased the RWC in the leaf blade of sour passion fruit plants (Figure 2A). Specifically, there was a reduction of 4.31% for every unit increase in ECw. When comparing the RWC of plants exposed to water salinity at 3.0 dS m^{-1} with those receiving the lowest salinity level of 0.6 dS m^{-1}, a decrease of 10.63% was observed.

This decline in RWC reflects the loss of tissue turgidity, attributed to osmotic stress caused by salinity. This stress factor impedes the plant's ability to absorb and transport water from the soil, significantly affecting plant growth and metabolism (Skider et al., 2020). Additionally, reduced water content in plant tissues leads to stomatal closure, serving as a defense mechanism against water loss through transpiration, thereby impacting key physiological processes such as stomatal conductance, intercellular CO_2 concentration, and photosynthesis (Figueiredo et al., 2019). A similar trend was also observed by A. M. de S. Silva Neta et al. (2020) in their study on the 'BRS Rubi do Cerrado' sour passion fruit, where increasing water salinity levels led to a reduction in relative water content in the leaf blade, at a rate of 2.91% per unit increase in ECw.

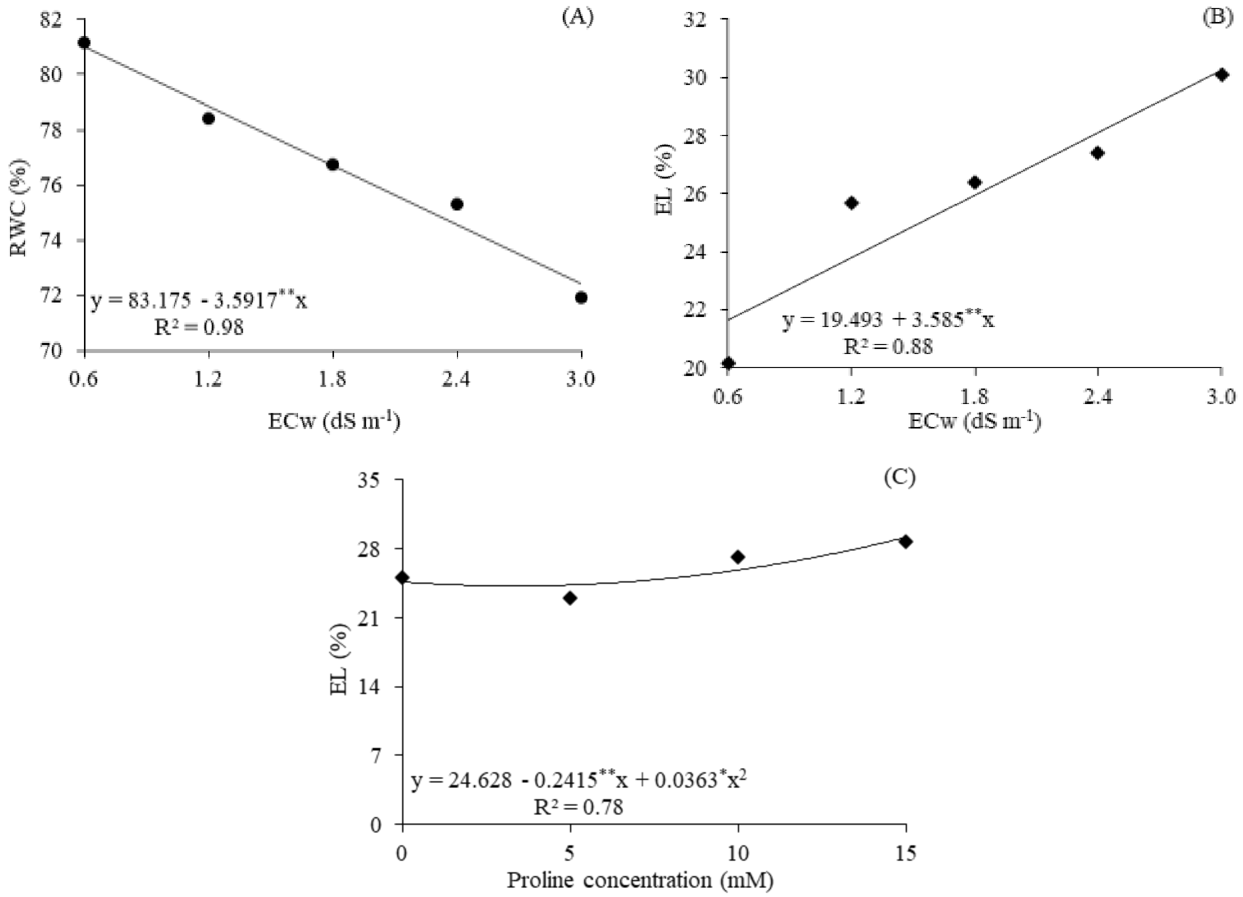

Figure 2. Relative water content in the leaf blade (RWC; A) and electrolyte leakage (EL; B and C) in sour passion fruit plants as a function of water salinity (ECw) and proline concentrations, at 66 days after sowing (DAS).
** - Significant at $p \leq 0.01$ by the F test.

Conversely, while RWC exhibited a linear decline (Figure 2A), the increase in saline water levels was associated with an increase in electrolyte leakage in the leaf blade of sour passion fruit plants (Figure 2B). Specifically, there was an 18.39% increase for every unit increase in ECw. When comparing the EL of plants irrigated with water at 3.0 dS m^{-1} with those grown under ECw of 0.6 dS m^{-1}, a substantial increase of 39.75% was observed. This effect is indicative of critical implications, suggesting that the accumulation of Na$^+$ and Cl$^-$ in the soil adversely affects the integrity of the plasma membrane (Zahedi et al., 2023). Furthermore, ionic toxicity triggers nutritional imbalance, potentially leading to Ca+ deficiency and consequently affecting cell wall formation, ultimately resulting in increased electrolyte leakage, as observed by Wanderley et al. (2020) in yellow passion fruit under saline water irrigation coupled with nitrogen fertilization, where ECw of 3.1 dS m^{-1} resulted in a 24.65% increase in EL compared to the salinity level of 0.3 dS m^{-1}.

Proline application led to an increase in electrolyte leakage in the leaf blade (Figure 2C), with the highest value (29.17%) observed in sour passion fruit plants subjected to a proline concentration of 15 mM. In relative terms, this corresponded to an 18.45% increase in EL for plants subjected to 15 mM proline compared to those exposed to 0 mM. This suggests that elevated proline concentrations may influence the permeability of the cell wall, consequently inducing an increase in electrolyte leakage. As noted by Cacefo et al. (2021), determining the optimal proline concentration is crucial, as excessive application can potentially promote or exacerbate toxicity, particularly under conditions of plant stress.

The effect of salt levels and proline concentrations was significant across all gas exchange variables in sour passion fruit plants measured at 66 days after sowing (Table 3). The interaction between the factors (SL × PRO) significantly influenced only the intercellular CO_2 concentration (*Ci*) of the sour passion fruit plants.

Table 3

Summary of analysis of variance regarding stomatal conductance (*gs*), transpiration (*E*), intercellular CO_2 concentration (*Ci*), CO_2 assimilation rate (*A*), instantaneous carboxylation efficiency (*iCE*), and instantaneous water use efficiency (*iWUE*) of passion fruit plants grown under water salinity and proline concentrations, at 66 days after sowing (DAS)

Source of variation	DF	Mean square					
		gs	*E*	*Ci*	*A*	*iCE*	*iWUE*
Salt level (SL)	4	0.016**	2.44**	25962.56**	38.07**	0.0176**	1.54**
Linear regression	1	0.065**	9.69**	100851.80**	150.75**	0.068**	4.97**
Quadratic regression	1	0.001^{ns}	0.05ns	1395.00*	0.18^{ns}	0.0013**	0.65^{ns}
Proline concentration (PRO)	3	0.008*	0.42**	2002.61**	87.14**	0.0026**	5.16**
Linear regression	1	0.014*	0.22*	5602.52**	16.46*	0.000013^{ns}	5.67**
Quadratic regression	1	0.007*	0.80**	357.01^{ns}	199.39**	0.0063**	7.98**
Interaction (SL × PRO)	12	0.0003^{ns}	0.009^{ns}	1268.23**	0.82^{ns}	0.000082^{ns}	0.23^{ns}
Residual	60	0.001	0.045	170.67	2.09	0.000182	0.33
CV (%)		21.03	7.01	7.36	7.95	12.34	9.57

DF - degrees of freedom; CV - coefficient of variation; (*) significant at p ≤ 0.05; (**) significant at p ≤ 0.01 probability; (ns) not significant.

Stomatal conductance in the passion fruit plants exhibited a linear reduction with increasing water salinity levels (Figure 3A), with a decrease of 14.10% for each unit increase in ECw. Comparing the stomatal conductance of plants subjected to the highest saline water level with those grown under water salinity of 0.6 dS m^{-1}, a considerable decline of 36.99% (0.084 mol H_2O m^{-2} s^{-1}) was observed.

In response to salt stress, many plants employ a strategy of partial stomatal closure to mitigate water loss. This defensive mechanism involves decreasing gs, as observed by A. A. R. da Silva et al. (2019b) in yellow passion fruit plants (*Passiflora edulis* F. flavicarpa) subjected to an ECw of 2.8 dS m^{-1}, resulting in a 50% decrease in gs compared to the lowest salinity level (0.7 dS m^{-1}). In sugar apple (*Annona squamosa* L.), E. M. da Silva et al. (2018) noted a 12.32% decline in gs under an ECw of 3.5 dS m^{-1} compared to the lowest salinity level of 0.5 dS m^{-1}.

Transpiration (E) also exhibited a linear decrease with rising water salinity levels (Figure 3B), with a 3.09% reduction for each unit increase in ECw. Plants subjected to an ECw of 3.0 dS m^{-1} displayed a decrease in E of 0.280 mmol H_2O m^{-2} s^{-1} (7.57%) compared to those irrigated with the least saline water (0.6 dS m^{-1}). In response to osmotic stress stemming from salt accumulation in the root zone, plants limit water loss by closing their stomata (E. M. da Silva et al., 2018). In a study examining gas exchange in sour passion fruit under varying saline water conditions (0.7, 1.4, 2.1, and 2.8 dS m^{-1}), A. A. R. da Silva et al. (2019) observed increased leaf transpiration at a water salinity of 1.4 dS m^{-1}.

The stomatal conductance and transpiration of sour passion fruit benefited from foliar application of proline, with estimated peak values of 0.2011 and 3.165 mmol H_2O m^{-2} s^{-1}, respectively, achieved at proline concentrations of 4.5 and 6.4 mM (Figure 3B and 3D). Proline, an amino acid, plays a role in various physiological processes, including stomatal regulation, gs control, and reduction of water loss through transpiration (El-Moukhtari et al., 2020). This effect was also observed by Leite et al. (2022) in *Physalis peruviana* L., where foliar application of 20 mM proline improved stomatal conductance and transpiration.

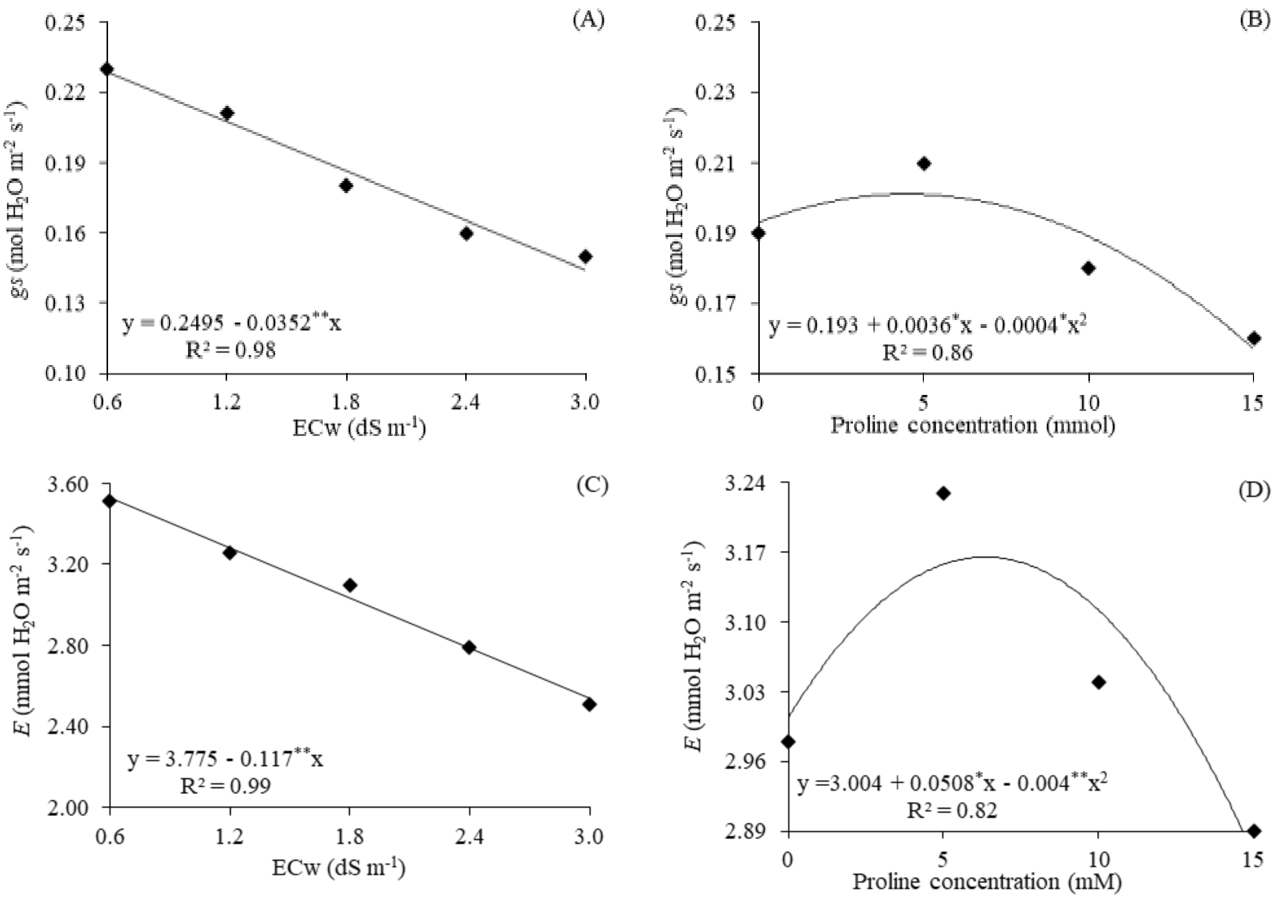

Figure 3. Stomatal conductance (*gs*; A and B) and transpiration (*E*; C and D) of sour passion fruit plants as a function of water salinity (ECw) and proline concentrations, at 66 days after sowing (DAS).
*, ** - significant at $p \leq 0.05$ and at $p \leq 0.01$ by F test, respectively.

Foliar application of proline increased the intercellular CO_2 concentration up to 10 mM (maximum value of 203.2889 μmol CO_2 m^{-2} s^{-1}) in sour passion fruit plants subjected to an ECw of 3.0 dS m^{-1} (Figure 4A). Exogenous proline application enhances the plant's ability to withstand salt stress by mitigating ion toxicity and influencing the expression of genes responsible for ion homeostasis (El-Moukhtari et al., 2020). Elevated proline concentration also stimulates the activity of enzymes involved in the plant's defense mechanisms against oxidative stress induced by an accumulation of ROS, thereby improving physiological processes (Tabssum et al., 2019).

Salinity negatively impacted the CO_2 assimilation rate of the passion fruit plants (Figure 4B), which exhibited a 7.66% reduction for each unit increase in ECw. When comparing the CO_2 assimilation rate of plants irrigated with an ECw of 3.0 dS m^{-1} to those with an ECw of 0.6 dS m^{-1}, a decrease of

19.27% (3.88 μmol CO_2 m^{-2} s^{-1}) was observed. This reduction in the CO_2 assimilation rate is directly related to the observed decrease in *gs* and transpiration, as stomatal closure limits CO_2 absorption and consumption in the substomatal chamber, thus impairing photosynthesis (Lacerda et al., 2022; Pinheiro et al., 2022). Excess salts in water and/or soil trigger a cascade effect, leading to osmotic stress; ionic stress, which causes toxicity and nutritional imbalances; and oxidative stress from the accumulation of ROS, which hampers the functioning of proteins and enzymes involved in photosynthesis (Arif et al., 2020). Conversely, foliar application of proline enhanced the CO_2 assimilation rate, reaching a maximum value of 20.211 μmol CO_2 m^{-2} s^{-1} in plants treated with 8.15 mM proline, with further reductions observed beyond this concentration (Figure 4C).

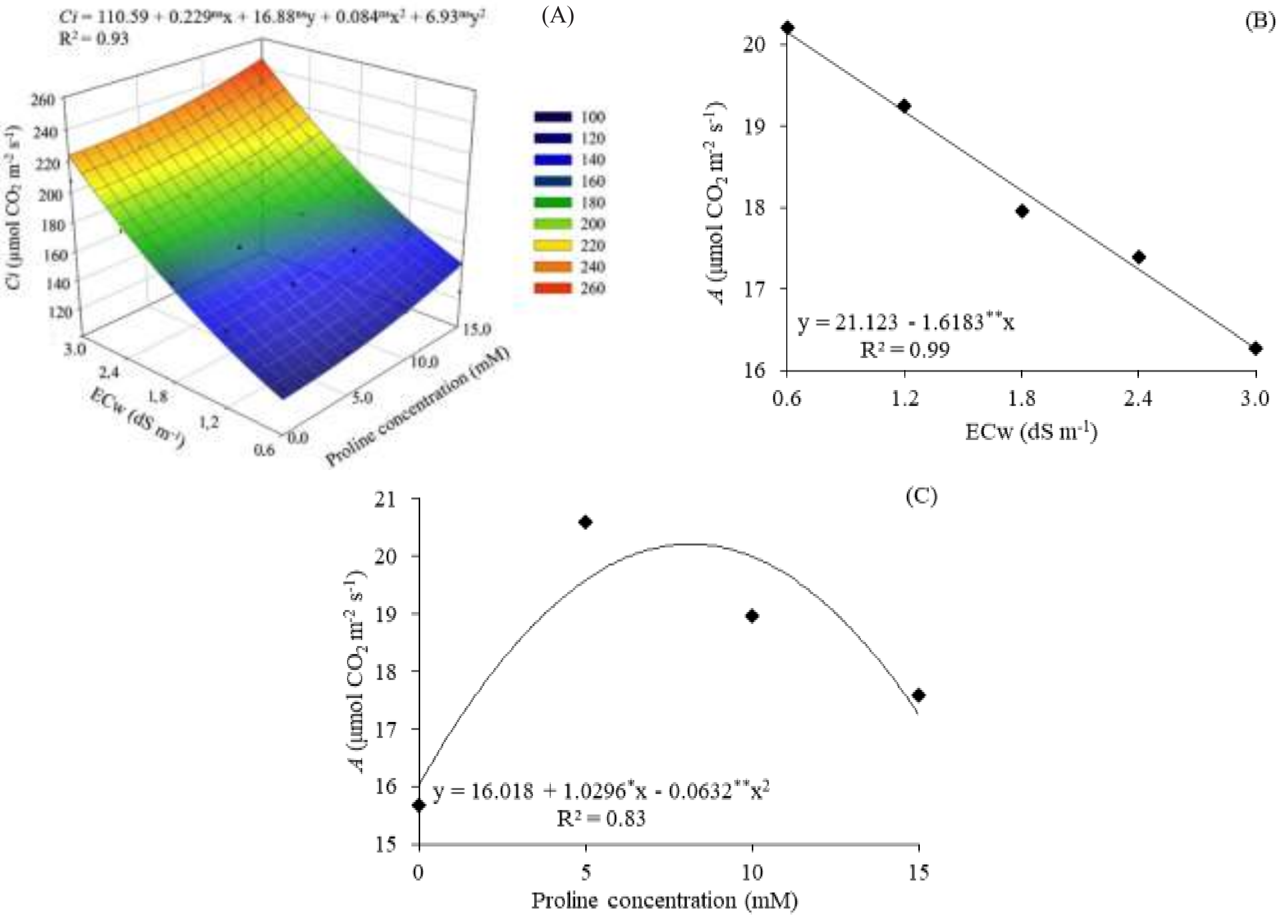

Figure 4. Intercellular CO_2 concentration (*Ci*; A) and CO_2 assimilation rate (*A*; B and C) of sour passion fruit plants as a function of water salinity (ECw) and proline concentrations, 66 days after the sowing (DAS).
ns, *, ** - not significant, significant at $p \leq 0.05$, and significant at $p \leq 0.01$ by the F test, respectively. X and Y - water electrical conductivity (ECw) and proline concentration, respectively.

The instantaneous carboxylation efficiency (*iCE*) of the passion fruit plants declined with increasing salinity of the irrigation water, displaying a 19.44% reduction for each unit increment (Figure 5A). When comparing the iCE of plants subjected to an ECw of 3.0 dS m^{-1} with those irrigated with an ECw of 0.6 dS m^{-1}, a reduction of 52.84% was noted. This decrease is directly linked to the decline in the CO_2 assimilation rate caused by salt stress, which limits the intercellular concentration of CO_2 in the substomatal chamber and the instantaneous carboxylation efficiency, as observed by Lima et al. (2019) with acerola (*Malpighia emarginata*) plants exposed to an ECw of 4.5 dS m^{-1}. A. A. R. da Silva et al. (2019) found similar reductions of 43% in iCE in yellow passion fruit (*Passiflora edulis*) under irrigation with water having an ECw of 2.8 dS m^{-1}.

Foliar application of proline enhanced *iCE* and *iWUE* up to concentrations of 7.2 and 9.4 mM, with maximum values of 0.1169 [(μmol CO_2 m^{-2} s^{-1}) (μmol CO_2 m^{-2} s^{-1}) $^{-1}$] and 6.4687 [(μmol CO_2 m^{-2} s^{-1}) (μmol CO_2 m^{-2} s^{-1}) $^{-1}$], representing increases of 13.2% and 17.2%, respectively, in relation to plants in the control treatment (Figure 5B and 5D). This effect is associated with proline's role in improving *gs* and CO_2 assimilation, resulting in better stomatal regulation and increased CO_2 assimilation, in addition to enhancing water content in plant tissues (Semida et al., 2020).

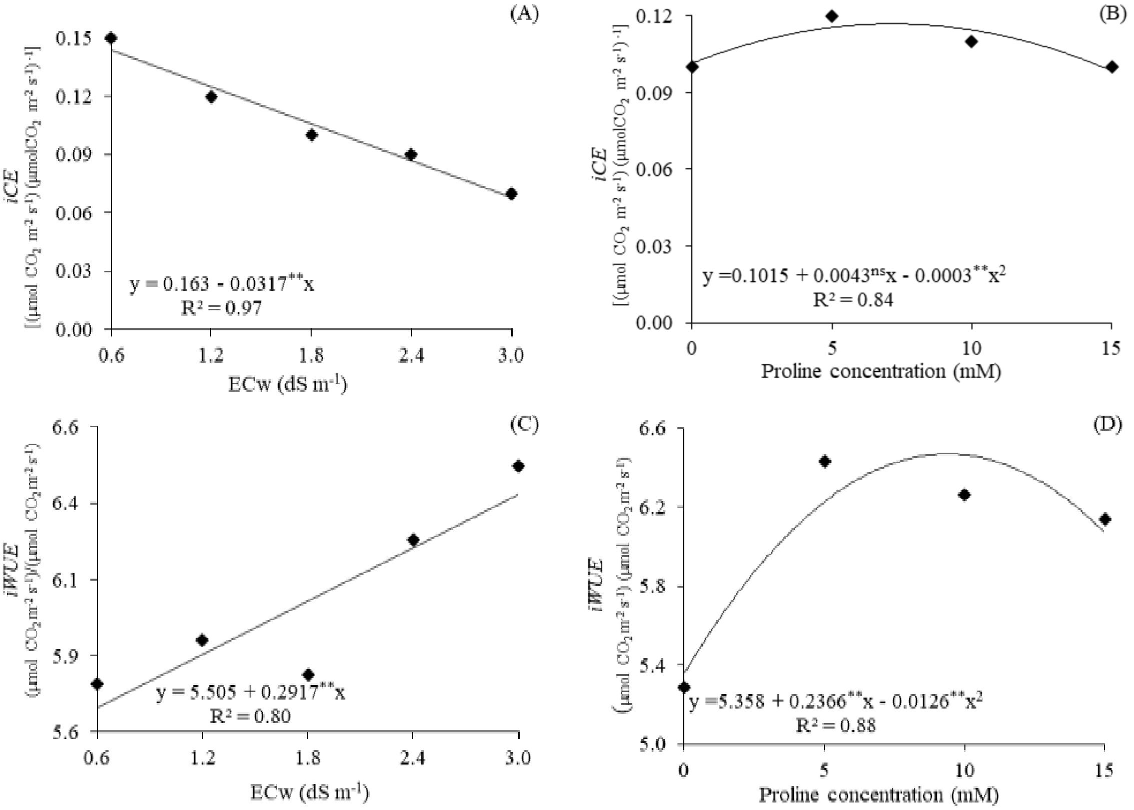

Figure 5. Instantaneous carboxylation efficiency (*iCE*; A and B) and instantaneous water use efficiency (*iWUE*; C and D) of sour passion fruit plants as a function of water salinity (ECw) and proline concentrations, at 66 days after sowing (DAS).
ns, *, ** - not significant, significant at $p \leq 0.05$, and significant at $p \leq 0.01$ by the F test, respectively.

Instantaneous water use efficiency (*iWUE*) exhibited an increase in plants subjected to increasing levels of irrigation water salinity, with a 5.29% increase per unit increment in ECw (Figure 5C). When comparing *iWUE* in plants subjected to an ECw of 3.0 dS m^{-1} to those receiving water with an ECw of 0.6 dS m^{-1}, a significant 12.32% increase was observed. Under conditions of water deficiency imposed by osmotic stress resulting from salinity, plants may develop morphological adaptations, reducing leaf area and minimizing water loss through evapotranspiration. This leads to enhanced water use efficiency by the plant (Ramezanifar et al., 2021). Similar findings were reported by Fátima et al. (2022) in their research on sugar apple seedlings subjected to increasing salinity of irrigation water and nitrogen fertilization, demonstrating a 10.42% increase in plants irrigated with an ECw of 5.0 dS m^{-1} (corresponding to 2.49 [(μmol CO_2 m^{-2} s^{-1}) / (μmol CO_2 m^{-2} s^{-1})] compared to those irrigated with the lowest conductivity (0.5 dS m^{-1}).

A significant effect ($p \leq 0.01$) of both water salinity levels and proline concentrations on the contents of chlorophyll a (Cl *a*), b (Cl *b*), total (Cl *t*), and carotenoids in sour passion fruit plants was evident 66 days after sowing. The interaction between these factors significantly influenced ($p \leq 0.01$) only the carotenoid contents of the sour passion fruit plants (Table 4).

Table 4

Summary of the analysis of variance regarding the chlorophyll a (Cl *a*), chlorophyll b (Cl *b*), total chlorophyll (Cl *t*), and carotenoid contents of sour passion fruit plants grown under water salinity and proline concentrations, at 66 days after sowing (DAS)

Source of variation	DF	Mean square			
		Cl a	*Cl b*	*Cl t*	*Carotenoids*
Salt level (SL)	4	59195.24**	258.14**	63913.38**	13574.47**
Linear regression	1	148309.16**	0.03^{ns}	148169.75**	52483.14**
Quadratic regression	1	67071.06**	607.43**	80445.78**	1214.62**
Proline concentration (PRO)	3	55681.97**	781.00**	69543.35**	292.49**
Linear regression	1	66642.19**	1172.61**	85488.69**	452.32**
Quadratic regression	1	58887.83**	567.91**	71021.14**	325.46**
Interaction (SL × PRO)	12	1077.71^{ns}	28.91^{ns}	932.44^{ns}	13.48**
Residual	60	422.36	30.54	514.65	5.17
CV (%)		4.72	5.94	4.29	1.36

DF - degrees of freedom; CV - coefficient of variation; (*) significant at $p \leq 0.05$; (**) significant at $p \leq 0.01$ probability; (ns) not significant.

In the case of Cl *a* content, an increase was observed up to an ECw of 1.3 dS m^{-1}, reaching a value of 483.35 µg mL^{-1}, followed by declines with increasing salinity of the irrigation water, leading to a minimum estimated value of 339.89 µg mL^{-1} (Figure 6A). This increase may be associated with the osmotic adjustment capacity of sour passion fruit that allows it to tolerate salinities up to 1.3 dS m^{-1}. Nevertheless, it is noteworthy that increasing ECw up to 3.0 dS m^{-1} resulted in a 29.7% decrease, indicating that salt stress detrimentally affected chlorophyll synthesis. Generally, high salt content in water inhibits the activity of 5-aminolevulinic acid, a chlorophyll precursor, and increases the activity of chlorophylase, which degrades pigment molecules, causing damage to chloroplasts and limiting pigmentation protein activity (Cavalcante et al., 2011).

Chlorophyll b content displayed stimulation in response to irrigation water salinity, with increases occurring up to an ECw of 1.8 dS m^{-1}, reaching 96.38 µg mL^{-1}, followed by decreases beyond this salinity level (Figure 6C). Lima et al. (2021) reported a 77% reduction in Cl b content in sour passion fruit at a salinity of 2.8 dS m^{-1}. In contrast, Andrade et al. (2022) found that salinity of 2.8 dS m^{-1} increased Cl b levels in yellow passion fruit.

Proline application led to elevated levels of Cl *a* and Cl *b*, with the highest estimated maximum values of 475.42 and 97.52 µg mL^{-1}, respectively, observed in plants subjected to concentrations of 5.1 and 4.3 mM (Figure 6B and 6C). Proline acts as an antioxidant, interacts with multiple enzymes, preserves protein activity, and may be involved in the regulation of genes related to chlorophyll biosynthesis (El-Betalgi et al., 2020). This could explain the observed positive effect on chlorophyll a and b levels in this study.

Total chlorophyll (Cl *t*) synthesis was stimulated by irrigation water salinity, with the maximum estimated value observed in plants subjected to an ECw of 1.2 dS m^{-1} (573.05 µg mL^{-1}), followed by declines beyond this level of water electrical conductivity (Figure 7A). This effect is linked to the plant's ability to adapt to salt stress by rapidly synthesizing chlorophyll to facilitate the capture and dissipation of light energy, as noted by Fátima et al. (2022) in *Annona squamosa* L.

As seen in the levels of chlorophylls a and b (Figure 6B and 6C), foliar application of proline increased total chlorophyll levels, with the highest value recorded at a concentration of 1.3 mM, reaching 578.58 µg mL^{-1} (Figure 7B). This increase in chlorophyll levels in passion fruit plants is attributed to proline reducing the activity of the enzyme chlorophylase, which is involved in the degradation of photosynthetic pigments (Butt et al., 2020).

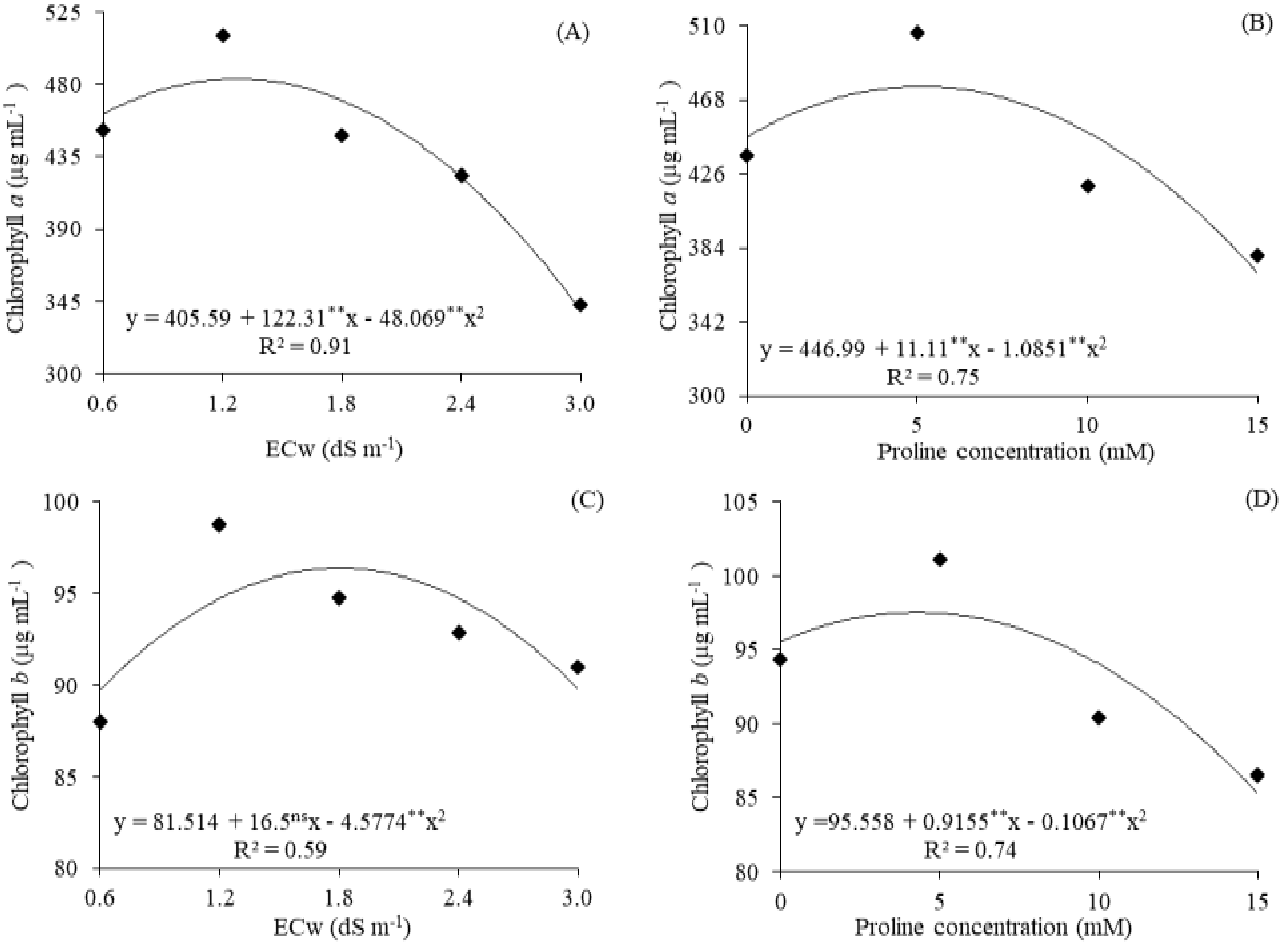

Figure 6. Chlorophyll a (Cl *a*; A and B) and chlorophyll b (Cl *b*; C and D) contents of sour passion fruit plants as a function of water salinity (ECw) and proline concentrations at 66 days after sowing (DAS).
ns, *, ** - not significant, significant at $p \leq 0.05$, and significant at $p \leq 0.01$ by the F test, respectively.

Regarding carotenoid levels, proline application mitigated the effects of salinity, resulting in the greatest increase (μg mL^{-1}) in plants subjected to an ECw of 0.6 dS m^{-1} and a proline concentration of 2.9 mM (Figure 7C). This effect is linked to proline's functions in inducing the biosynthesis of photosynthetic pigments and its ability to alleviate salt stress, increasing the presence of antioxidants that protect against oxidative damage, thus stabilizing chloroplast membranes and preserving photosystem activity (El-Shawa et al., 2020).

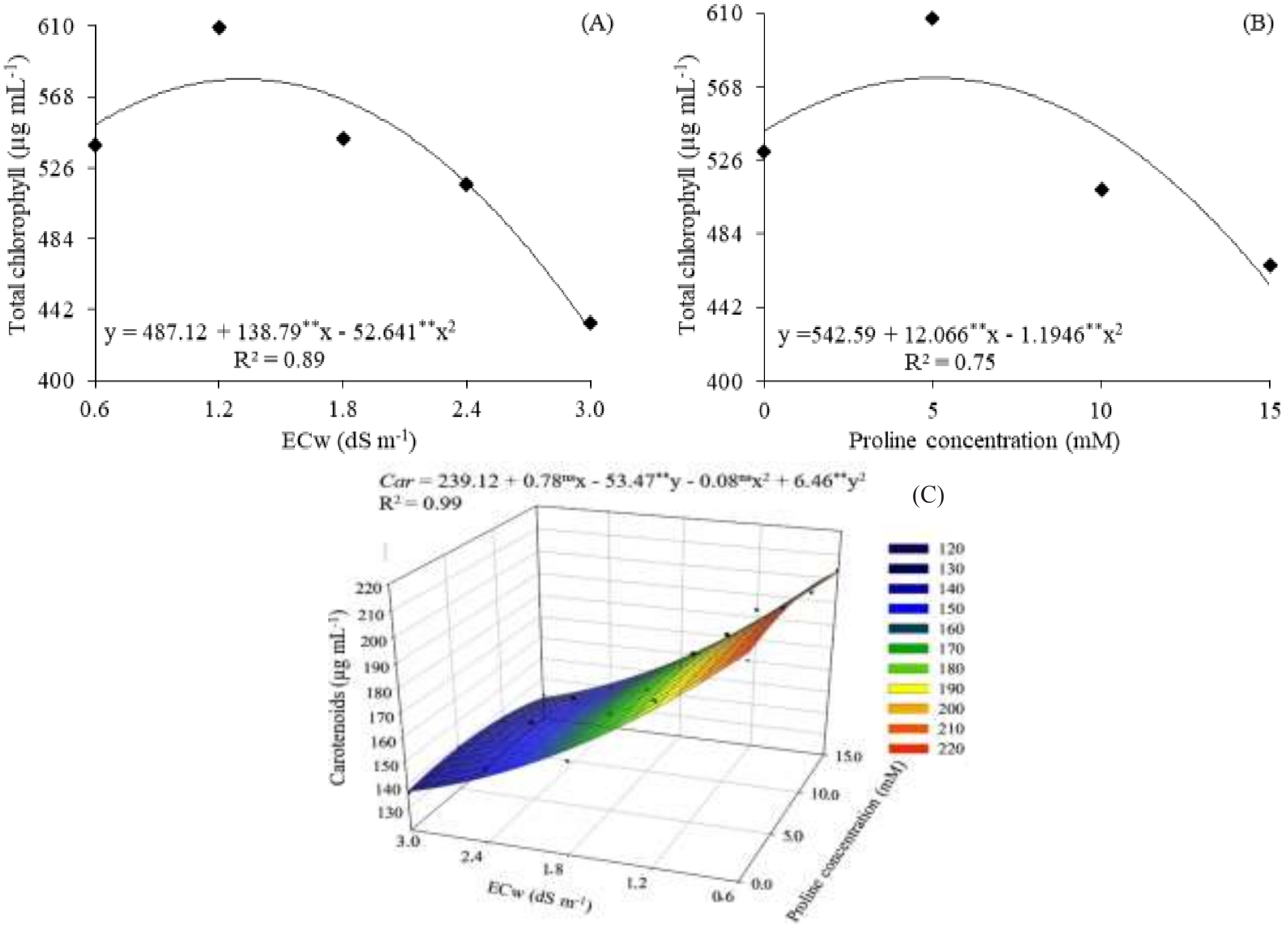

Figure 7. Total chlorophyll (Cl *t*; A and B) and carotenoid (*Car*; C) contents of sour passion fruit plants as a function of water salinity (ECw) and proline concentrations, at 66 days after sowing (DAS).
** - Significant at $p \leq 0.01$ by the F test; X and Y - water electrical conductivity (ECw) and proline concentration, respectively.

Conclusion

Water salinity levels from 0.6 dS m^{-1} reduce relative water content, disrupt gas exchange, and increase electrolyte leakage in the leaf blades of 'BRS GA1' sour passion fruit plants.

Irrigation within the electrical conductivity range of 1.3 to 1.8 dS m^{-1} fosters the synthesis of photosynthetic pigments in 'BRS GA1' sour passion fruit plants, as observed 66 days after sowing.

Foliar application of proline at concentrations ranging from 4.5 to 6.5 mM increases stomatal conductance, transpiration, CO_2 assimilation rate, instantaneous carboxylation efficiency, and chlorophyll synthesis in sour passion fruit plants, evidenced 66 days after sowing.

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