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Calcium pyruvate as a salt stress mitigator in yellow passion fruit seedlings[1]

Piruvato de cálcio como mitigador do estresse salino em mudas de maracujazeiro amarelo

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HIGHLIGHTS:

Foliar spraying of pyruvate at a concentration of 50 µM improves the morphophysiology of passion fruit seedlings.
Application of calcium pyruvate in passion fruit seedlings reduces the effects of salt stress on photosynthesis.
Pyruvate supplementation protects against electrolyte leakage and improves water relations.

ABSTRACT: Although the semi-arid region of Northeast Brazil is a major producer of yellow passion fruit, the problems of salts in the soil and water sources, in many areas have limited the growth and production of this crop, which highlights the importance of studies aimed at reducing such effects. In this context, the objective of this study was to evaluate the effect of foliar application of pyruvate, as a mitigator of salt stress, on the morphophysiology of yellow passion fruit, in seedling phase. The treatments consisted of three electrical conductivities of irrigation water (EC_w: 0.8, 2.4, and 4.0 dS m^{-1}) and three concentrations of pyruvate (0, 25, and 50 mM), distributed in a randomized block experimental design in a 3 × 3 factorial scheme, with four replications and two plants per plot. Irrigation with EC_w of 4.0 dS m^{-1} reduces growth variables, phytomass, Dickson quality index, and increases electrolyte leakage in passion fruit seedlings cv. Redondo Amarelo. Exogenous application of calcium pyruvate (25 and 50 mM) increased growth, phytomass, Dickson quality index, relative water content and leaf succulence and reduced electrolyte leakage in the leaf blade in passion fruit. Exogenous application of pyruvate attenuates salt stress, with beneficial effects on CO_2 assimilation rate, transpiration, instantaneous carboxylation efficiency, intrinsic water use efficiency, and root dry mass.

Key words: *Passiflora edulis* f. flavicarpa Deneger, salt stress, physiology

RESUMO: Embora a região semiárida do Nordeste brasileiro seja uma grande produtora de maracujá amarelo, os problemas de sais no solo e nas fontes hídricas, em muitas áreas, têm limitado o crescimento e a produção dessa cultura, o que realça a importância de estudos visando a reduzir tais efeitos. Nesse contexto, objetivou-se com este estudo, avaliar o efeito da aplicação foliar de piruvato, como mitigador do estresse salino, sobre a morfofisiologia do maracujazeiro cv. Redondo Amarelo, em fase de mudas. Os tratamentos constaram de três condutividades elétricas da água de irrigação (CEa: 0,8, 2,4 e 4,0 dS m^{-1}) e três concentrações de piruvato (0, 25 e 50 mM), distribuídos em delineamento experimental de blocos casualizados, em esquema fatorial 3 × 3, com quatro repetições e duas plantas por parcela. A irrigação com águas de CEa de 4,0 dS m^{-1} reduz as variáveis de crescimento, fitomassa, indice de qualidade de Dickson e aumenta o extravasamento de eletrólitos em mudas de maracujazeiro cv. Redondo Amarelo. A aplicação exógena de piruvato de cálcio (25 e 50 mM) favorece as variáveis de crescimento, fitomassa, indice de qualidade de Dickson, teor relativo de água, suculência foliar e reduz o extravasamento de eletrólitos no limbo foliar do maracujá. A aplicação exógena de piruvato atenua o estresse salino, com efeitos benéficos na taxa de assimilação de CO_2, transpiração, eficiência da carboxilação instantânea, eficiência intrínseca do uso da água e massa seca das raízes.

Palavras-chave: *Passiflora edulis* f. flavicarpa Deneger, estresse salino, fisiologia

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Introduction

Yellow passion fruit (*Passiflora edulis* f. flavicarpa Degener) is one of the main agricultural crops commercially exploited in the Brazilian semiarid region (Silva et al., 2021). The edaphoclimatic conditions in this region, in general, are suitable for the cultivation of passion fruit, except rainfall, which in many areas is irregular and poorly distributed, without meeting the needs of the plants. In most of the wells drilled for water sources in the Brazilian semiarid region, the waters contain high concentrations of salts, at levels that are harmful to many crops (Silva et al., 2022).

Under such conditions, morphological, physiological, and biochemical changes occur in plants, due to the difficulty of water absorption, its low potential energy, ion toxicity, and nutritional imbalance, with consequences in the reduction of growth and development of the plants (Munns & Tester, 2008; Ma et al., 2020). The scientific community is interested in developing technologies to attenuate the effects of salt stress on plants, which can enable the use of saline water. Pyruvate is one of the products that can be used.

Coming from glycolysis, pyruvate is crucial in the metabolism of the Krebs cycle and the respiratory chain, resulting in the production of ATP molecules, vital for development in plants (Taiz et al., 2017). Exogenous application of pyruvate may favor the energy mechanisms of passion fruit. With this supplementation, part of the energy that would be spent in glycolysis for the production of pyruvic acid is used in processes of adaptation to salt stress. Research with pyruvate began in recent years, in a study carried out in China (Shen et al., 2017). In Brazil, the research group of this work started the first assays, with promising results in the spraying of leaves of peanut plants (Barbosa et al., 2021). In this context, the objective of this study was to evaluate the effect of foliar application of pyruvate as a mitigator of salt stress on the morphophysiology of yellow passion fruit cv. Redondo Amarelo in seedling phase.

Material and Methods

The study was carried out from April to June 2021, in a greenhouse, at the Center of Technology and Natural Resources, belonging to UFCG, in Campina Grande, PB, Brazil (07° 15' 18" S, 35° 52' 28" W, and average attitude of 550 m). The temperature and relative humidity of air data collected outside the greenhouse during the research period are shown in Figure 1.

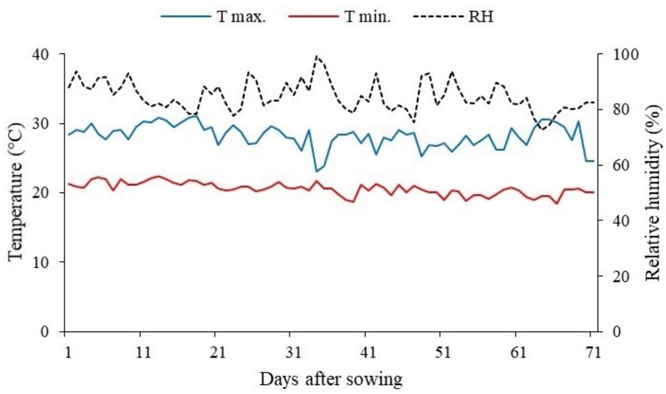

Figure 1. Maximum temperature (T max.), minimum temperature (T min.) (°C), and average relative humidity of air (RH), observed during the experimental period

The treatments consisted of a combination of two factors: three levels of electrical conductivity of the irrigation water (ECw: 0.8, 2.4, and 4.0 dS m^{-1}), associated with three concentrations of pyruvate (0, 25, and 50 mM), using calcium pyruvate as a source. The design was in randomized blocks, in a 3 × 3 factorial scheme, with four replications (36 plots), and the experimental unit consisted of two plants per plot.

Pyruvate concentrations were based on a study conducted by Shen et al. (2017) with *Arabidopsis* dealing with exogenous application of the product. An adjustment was made in the concentration of pyruvate, given that the original research was in a sample of leaves incubated in a pyruvate solution at concentrations of 10, 100, and 1000 μM in an uncultivated species (*Arabidopsis*).

The plots consisted of plastic bags, with capacity of 1.0 dm^3 (20 × 25 cm). The plastic bags were filled with soil of sandy loam texture, classified as Entisol, collected at 0-0.30 m depth, from the municipality of Lagoa Seca, Paraíba, Brazil, whose physical and chemical attributes were determined according to the methodology described by Teixeira et al. (2017) (Table 1).

The saline waters were prepared by dissolving the salts NaCl, $CaCl_2.2H_2O$, and $MgCl_2.6H_2O$, in equivalent proportions of 7:2:1, respectively, in the local municipal supply water (ECw = 0.4 dS m^{-1}), based on the relationship between ECw and salt concentration ($mmol_c$ L^{-1} = 10 × ECw), reported by Richards (1954). This proportion of salts is commonly found in water sources used for irrigation, in small properties in the Brazilian Northeast (Medeiros, 1992).

Seeds of sour passion fruit cv. Redondo Amarelo, were used in this study. According to the company Agristar, the cultivar has the characteristics of fruits with intense and smooth yellow skin color, very juicy and acidic pulp and average weight of 160 g.

Two passion fruit seeds were sown per pot. After emergence stabilization, at 20 days after emergence (DAE), thinning was performed, leaving only one plant per pot.

Before sowing, the soil moisture content was raised to the level corresponding to field capacity, with water from the local supply system. Irrigation management was based on the

Table 1. Chemical attributes of the soil material used in the experiment

pH	P	K	Ca	Na	Mg	Al	H	SB	CEC	V	m	OM
	(mg dm^{-3})	($cmol_c$ dm^{-3})								(%)		(g dm^{-3})
6.5	79	0.24	9.5	0.51	5.4	0	0.9	15.65	16.55	94.56	0	8.1

ECse	ESP	Particle size fraction (g kg^{-1})		
(dS m^{-1})	(%)	Sand	Silt	Clay
2.15	3.08	572.7	100.7	326.6

pH H_2O (1:2.5)- Hydrogen potential; OM - Organic matter; ECse - Electrical conductivity of the saturation extract; CEC - Cation exchange capacity at pH 7.0; ESP - Exchangeable sodium percentage weighing method, in which two pots of each treatment, with drains at the bottom, were initially saturated until they started to drain. After the drainage ceased, the pots were weighed to obtain the initial wet weight, corresponding to moisture content close to field capacity.

At 30 days after emergence (DAE), irrigation with saline water was started and continued until 70 DAE. A leaching fraction, equivalent to 10%, was applied at 10-day intervals, to avoid excessive accumulation of salts in the root zone.

Calcium pyruvate was purchased from American Pharm Supplements LLC. Pyruvate solutions of adequate concentrations were obtained by the dissolution of calcium pyruvate in distilled water, and prepared in each application event. The application of pyruvate began at 40 DAE, when the plants had been irrigated for 10 days with saline water. Six applications were performed with an interval of five days (at 40, 45, 50, 55, 60, and 65 DAE). With the aid of a sprayer, 40 mL of the solution was applied to each plant, starting at 5 p.m. To avoid solution drift, the plants were protected with plastic curtain during spraying, and the soil was covered with a blanket.

Fertilization with nitrogen, potassium, and phosphorus was performed based on the recommendation of Novais et al. (1991), applying per pot 0.555 g of urea, 1.25 g of monoammonium phosphate, and 0.625 g of potassium chloride, equivalent to 100, 300, and 150 mg dm^{-3} of soil of N, P, and K, respectively, in two applications, at 20 and 40 DAE. On the same occasions, a solution with a predominance of micronutrients at a concentration of 1.0 g L^{-1} of Dripsol Micro® was applied, containing: Mg (1.1%); Zn (4.2%); B (0.85%); Fe (3.4%); Mn (3.2%); Cu (0.5%); and Mo (0.05%), on the adaxial and abaxial surfaces of the leaves, using a spray bottle.

At 70 DAE, the relative water content (RWC), leaf succulence (SUC), and electrolyte leakage (EL), physiological parameters, growth, phytomass, and Dickson quality index were evaluated. RWC was estimated by the relationship between fresh mass (FM), turgid mass (TM), and dry mass (DM) of six leaf discs, using Eq. 1 (Barrs & Weatherley, 1962):

$$RWC = \frac{(FM - DM)}{(TM - DM)} \times 100 \quad (1)$$

where:

RWC - relative water content (%);
FM - leaf fresh mass (g);
DM - leaf dry mass (g); and,
TM - leaf turgid mass (g).

For the electrolyte leakage from the leaf blade, five leaf discs with dameter of 0.77 mm were collected from the middle third of the plants, washed with distilled water, aiming at the removal of other electrolytes adhered to the leaves, and placed in beakers with 50 mL of distilled water, which were then hermetically sealed with aluminum foil. The beakers were kept at 25 °C for 90 min, and then the determination of the initial electrical conductivity (ECi) was performed; afterward, the beakers were put in a forced-air oven at 80 °C for 90 min, after cooling, the final electrical conductivity was determined (ECf). In this manner, the EL was obtained according to Scotti-Campos et al. (2013), using Eq. 2:

$$EL = \frac{ECi}{ECf} \times 100 \quad (2)$$

where:

EL - electrolyte leakage in the leaf blade (%);
ECi - initial electrical conductivity (dS m^{-1}); and,
ECf - final electrical conductivity (dS m^{-1}).

Leaf succulence was determined using the methodology proposed by Mantovani (1999), based on Eq. 3:

$$SUC = \frac{(FM - DM)}{LA} \quad (3)$$

where:

SUC - leaf succulence (g cm^{-2});
FM - leaf fresh mass (g);
DM - leaf dry mass (g); and,
LA - leaf area (cm^2).

The physiological parameters were evaluated between 7 and 10 a.m. Stomatal conductance (gs) (mol m^{-2} s^{-1}), transpiration (E) (mmol H_2O m^{-2} s^{-1}), intercelluar CO_2 concentration (Ci) (μmol CO_2 mol^{-1}), and CO_2 assimilation rate (A) (μmol CO_2 m^{-2} s^{-1}), were evaluated using a portable infrared gas exchange analyzer (Infra Red Gas Analyzer-IRGA, from ADC BioScientific Ltd, model LC-Pro). Air temperature and CO_2 concentration assessments were performed under ambient conditions, and the luminosity was adjusted to 1200 μmol m^{-2} s^{-1} of radiation, using an artificial source provided with the equipment. Intrinsic carboxylation efficiency (CEi - A/Ci) ((μmol m^{-2} s^{-1})(μmol mol^{-1})$^{-1}$) and intrinsic water use efficiency ((WUEi) ((μmol m^{-2} s^{-1}) (mmol of H_2O m^{-2} s^{-1})$^{-1}$), were determined.

On the same date, plant height (PH- cm), number of leaves per plant (NL), stem diameter (SD - mm), measured 2 cm above the ground with the aid of a digital caliper, leaf area (LA - cm^2), root dry mass (RDM), shoot dry mass (ShDM), total dry mass (TDM) were determined. LA was determined by the ratio of the dry mass of the leaf discs (five discs per leaf) and the total dry mass of the leaves. Leaf discs were obtained using a hole puncher with a known area (1.41 cm^2), without coinciding with the central vein of the leaf, as described by Benincasa (2003).

The quality of passion fruit seedlings was determined using the Dickson Quality Index - DQI (Dickson et al., 1960), Eq. 4:

$$DQI = \frac{(TDM)}{\left(\frac{PH}{SD}\right) + \left(\frac{ShDM}{RDM}\right)} \quad (4)$$

where:

DQI - Dickson quality index;
PH - plant height (cm);
SD - stem diameter (mm);
TDM - total dry mass (g per plant);
ShDM - shoot dry mass (g per plant); and,
RDM - root dry mass (g per plant).

To determine phytomass, the plants were cut close to the soil surface and separated into shoot and roots. Subsequently, the different parts were placed in a paper bag and dried in a forced air oven, at a temperature of 65 °C, until reaching constant weight. Then, the plant material was weighed to obtain the values (g per plant) for root dry mass (RDM) and shoot dry mass (ShDM). The sum of RDM and ShDM resulted in the total dry mass (TDM) of the plant.

For statistical analyses, the data were preliminarily subjected to the normality test (Kolmogorov-Smirnov), followed by analysis of variance using the F test and, when significant, the Tukey test was applied, using the statistical software Sisvar (Ferreira, 2019).

Results and Discussion

According to the analysis of variance summary (Table 2), there was a significant effect of salinity on relative water content (RWC) and electrolyte leakage (EL). For the pyruvate factor, significant effects were recorded on RWC, SUC, and EL. There was no effect of the ECw × P interaction on the variables studied.

The increase in the electrical conductivity of the irrigation water (2.4 to 4.0 dS m^{-1}) reduced the relative water content (RWC) in the leaf by 5.42 and 6.27, respectively, in comparison to the plants irrigated with water with an electrical conductivity of 0.8 dS m^{-1} (Table 3).

Based on evidence found in the literature, such reductions are related to lower water absorption by plants, due to the osmotic effect of salts in the soil and accumulation of sodium in cells (Taiz et al., 2017; Andrade et al., 2019; Simões et al., 2021).

As a consequence of the decrease in the relative water content (RWC), the water saturation deficit increased in the treatments of ECw 2.4 and 4.0 dS m^{-1}. These results corroborate those of Silva Neta et al. (2021), who studied morphophysiology of the passion fruit 'BRS Rubi do Cerrado' irrigated with saline waters and nitrogen fertilization and found that EC_w of 3.5 dS m^{-1} reduced by 9.40% the relative water content of 'BR Rubi do Cerrado' compared to the treatment with the lowest salinity level (0.3 dS m^{-1}).

There was no effect on the succulence levels (SUC) caused by the salinity treatments, which can be explained by the very nature of the cellular tissues of passion fruit plant, which are not characterized as water storage (Ogburn & Edwards, 2010). Regarding the electrolyte leakage from the cells, with the use of water with an ECw of 2.4 dS m^{-1}, cell leakage did not differ significantly from the value obtained in the control. Greater cell damage was observed when the plants were irrigated with water of 4.0 dS m^{-1}, with an increase of 15.18% compared to the treatment with low salinity (0.8 dS m^{-1}) (Table 3). This increase in EL as a function of salinity may be related to the release of ions (electrolytes), that is, greater loss in integrity and destabilization of the cell membrane (Lima et al., 2021b).

Regarding the isolated effect of pyruvate, its application contributed to increasing the relative water content of the cells (RWC), with increase of 3.29% under the application of 50 mM, compared to the treatment without pyruvate. At this concentration, the degree of succulence increased by 26.72%, in the same comparison. Regarding electrolyte leakage (Table 3), the lowest damage occurred in plants subjected to exogenous application of 25 and 50 mM of pyruvate, with reductions of 8.16 and 15.80%, respectively, compared to the control.

These results, in general, corroborate those obtained by Lima et al. (2021a), when evaluating the effects of hydrogen peroxide on growth variables, water relations and photosynthetic pigments of passion fruit cv. BRS Rubi do Cerrado, as a function of the cationic nature of irrigation water.

Considering that it is more important to discuss the effects of interaction when significant, there were interactive effects between the factors (ECw × P) on all variables of gas exchange with the exception of the intercelular CO_2 concentration in the substomatal chamber (Ci) (Table 4). For this variable, the effect was only caused by water salinity, with a decrease in intercelular CO_2 concentration when the plants were irrigated with more saline waters, possibly due to stomatal closure, as it hinders the diffusion of CO_2 to the leaf tissues, or to the use of Ci in photosynthesis.

When analyzing the ECw × P interaction (Table 5), on gs the effect of pyruvate occurred only at the lowest salinity level. However, in relation to CO_2 assimilation rate (A), the application of pyruvate at a dose of 50 mM favored the reduction of CO_2 by increasing the synthesis of organic compounds, with an increase of 195% in comparison with the treatment without pyruvate, when the plant was irrigated with water at the highest concentration of salts (4.0 dS m^{-1}).

The benefits of pyruvate in mitigating salinity (4.0 dS m^{-1}) recorded in CO_2 assimilation rate were also reflected in

Table 2. Summary of the analysis of variance for relative water content (RWC), leaf succulence (SUC), and electrolyte leakage (EL) of the seedlings of passion fruit cv. Redondo Amarelo cultivated with saline waters and supplementation with calcium pyruvate, 70 days after emergence

Sources of variation	DF	Mean squares		
		RWC	SUC	EL
Blocks	3	2.39^{ns}	4.28^{ns}	5.44^{ns}
Salinity (ECw)	2	97.74**	5.62^{ns}	15.41**
Pyruvate (P)	2	32.54**	56.17**	21.18**
ECw × P interaction	4	2.04^{ns}	1.15^{ns}	1.19^{ns}
Residual	24	1.58	1.82	1.48
CV (%)	-	1.58	7.66	7.89

CV (%) - Coefficient of variation; DF - Degrees of freedom; ns, *, ** - Not significant, significant at $p \leq 0.05$ and at $p \leq 0.01$ by F test, respectively

Table 3. Means of relative water content (RWC), leaf succulence (SUC) and electrolyte leakage (EL) of cells of yellow passion fruit plants in seedling stage, as a function of irrigation with salinized water and exogenous application of calcium pyruvate, 70 days after emergence

Salinity (dS m^{-1})	Means		
	RWC (%)	SUC (g cm^{-2})	EL (%)
0.8	83.0 ± 0.34 a	18.05 ± 0.75 a	14.49 ± 0.38 b
2.4	78.50 ± 0.67 b	17.99 ± 0.68 a	15.11 ± 0.57 b
4.0	77.80 ± 0.57 b	16.83 ± 0.52 a	16.69 ± 0.52 a
Pyruvate (mM)	**Means**		
0	77.91 ± 0.87 b	15.79 ± 0.25 b	16.77 ± 0.22 a
25	80.42 ± 0.86 a	17.08 ± 0.41 b	15.40 ± 0.44 b
50	81.02 ± 0.60 a	20.01 ± 0.56 a	14.12 ± 0.64 c

In each variable, means with the same letter do not differ from each other by Tukey's test ($p \leq 0.05$)

Table 4. Summary of the analysis of variance for stomatal conductance (gs), transpiration (E), intercelluar CO_2 concentration (Ci), CO_2 assimilation rate (A), instantaneous carboxylation efficiency (CEi), and intrinsic water use efficiency (WUEi) of the seedlings of passion fruit cv. Redondo Amarelo cultivated with saline waters and supplementation with calcium pyruvate, 70 days after emergece

Sources of variation	DF	Mean squares					
		gs	E	Ci	A	CEi	WUEi
Blocks	3	5.14×10^{-4ns}	0.01^{ns}	72.76^{ns}	0.58^{ns}	2.20×10^{-5ns}	52.48^{ns}
Salinity (ECw)	2	$8.63 \times 10^{-3**}$	1.32^{**}	25420.18^{**}	11.80^{**}	4.23×10^{-22ns}	119.55^{*}
Pyruvate (P)	2	$2.10 \times 10^{-3*}$	0.25^{**}	1351.74^{ns}	39.67^{**}	$4.75 \times 10^{-4**}$	1230.71^{**}
ECw × P interaction	4	$1.34 \times 10^{-3*}$	0.13^{*}	667.31^{ns}	7.74^{**}	$1.25 \times 10^{-4**}$	210.59^{**}
Residual	24	4.20×10^{-4}	0.03	881.62	0.26	1.20×10^{-5}	33.97
CV (%)	-	13.01	9.84	10.34	9.66	17.18	17.17

CV (%) - Coefficient of variation; DF - Degrees of freedom; ns, *, ** - Not significant, significant at $p \leq 0.05$ and at $p \leq 0.01$ by F test, respectively

Table 5. Means of gas exchange parameters for stomatal conductance (gs - mol m^{-2} s^{-1}), transpiration (E - mmol H_2O m^{-2} s^{-1}), CO_2 assimilation rate (A - µmol CO_2 m^{-2} s^{-1}), instantaneous carboxylation efficiency (CEi - (µmol m^{-2} s^{-1}) (µmol mol^{-1})$^{-1}$), and intrinsic water use efficiency (WUEi - (µmol m^{-2} s^{-1}) (mmol of H_2O m^{-2} s^{-1})$^{-1}$) for the analysis of the interaction between salinity and pyruvate concentrations, and means for the individual effect of salinity on internal CO_2 concentration (Ci - µmol CO_2 mol^{-1}), in yellow passion fruit plants in seedling phase, under irrigation with salinized water and exogenous application of calcium pyruvate, 70 days after emergence

Variables	ECw (dS m^{-1})	Pyruvate (mM)		
		0	25	50
gs	0.8	0.14 ± 1.18×10^{-2} bA	0.21 ± 7.07×10^{-3} aA	0.20 ± 1.39×10^{-4} aA
	2.4	0.15 ± 7.07×10^{-3} aA	0.15 ± 1.24×10^{-2} aB	0.16 ± 2.27×10^{-2} aB
	4.0	0.13 ± 7.07×10^{-3} aA	0.14 ± 1.00×10^{-3} aB	0.12 ± 2.36×10^{-3} aB
E	0.8	1.92 ± 0.07 bA	2.45 ± 0.01 aA	2.49 ± 0.04 aA
	2.4	1.60 ± 0.18 bA	1.66 ± 0.09 abB	1.93 ± 0.09 aB
	4.0	1.72 ± 0.01 aA	1.69 ± 0.03 aB	1.68 ± 0.10 aB
A	0.8	3.10 ± 0.14 cB	5.97 ± 0.01 bA	9.30 ± 0.21 aA
	2.4	5.22 ± 0.08 aA	5.71 ± 0.28 aA	6.00 ± 0.00 aB
	4.0	2.01 ± 0.08 cC	4.71 ± 0.28 bB	5.93 ± 0.65 aB
CEi	0.8	9.41×10^{-3} ± 4.99×10^{-4} cB	1.79×10^{-2} ± 2.79×10^{-4} bA	2.83×10^{-2} ± 8.93×10^{-4} aA
	2.4	1.79×10^{-2} ± 8.83×10^{-4} aA	1.90×10^{-2} ± 8.17×10^{-4} aA	2.12×10^{-2} ± 4.97×10^{-4} aB
	4.0	8.04×10^{-3} ± 1.13×10^{-3} bB	2.01×10^{-2} ± 2.53×10^{-3} aA	2.77×10^{-2} ± 3.20×10^{-3} aA
WUEi	0.8	21.64 ± 2.23 bB	28.55 ± 1.06 bA	46.50 ± 1.06 aA
	2.4	35.00 ± 1.23 aA	37.94 ± 3.50 aA	39.83 ± 5.62 aA
	4.0	15.70 ± 1.36 cB	33.66 ± 2.04 bA	46.71 ± 4.72 aA
	Means for the individual factor 'Salinity' (dS m^{-1})			
Ci	0.8		2.4	4.0
	330.66 ± 3.20 A		292.11 ± 4.95 B	239.00 ±12.95 C

Means with the same lowercase letters between doses of pyruvate do not differ significantly from each other and means with the same uppercase letters between salinity levels do not differ significantly from each other by the Tukey test ($p \leq 0.05$)

the instantaneous carboxylation efficiency (CEi), but with attenuating effect only at the lowest concentration of salts (ECw: 0.8 dS m^{-1}). The opposite happened with the intrinsic water use efficiency (WUEi), greatly favored by pyruvate at the highest dose (50 mM), when the plants were irrigated with more saline water (4.0 dS m^{-1}), with increment of 198%, compared to the control. This increase was due to photosynthesis because, at the highest concentration of pyruvate and at the highest salinity, the stomata did not close. It should be noted that one of the main mechanisms that plants use to reduce water loss in such situations is stomatal closure (Lima et al., 2022), which is indicative, in this study, of salinity mitigation effects by pyruvate.

Such benefits must be associated with the maintenance of water balance and greater availability of NADPH, ATP, and substrate for the regeneration of RuBisCO, in the carbon cycle in C3 plants (Taiz et al., 2017). As a consequence, the protective effect of pyruvate in maintaining the photosynthetic activity of passion fruit seedlings is noticeable, because in situations of its reduction, resulting from stomatal closure, photochemical damage to the photosynthetic apparatus can occur, as there is no flow of energy between the various processes, with CO_2 reduction and synthesis of organic compounds (Munns & Tester 2008; Taiz et al., 2017).

Transpiration was also significantly affected by the interaction between irrigation water salinity and pyruvate concentrations (Table 5). It was verified that plants subjected to 25 and 50 mM of pyruvate and irrigated with water of 0.8 dS m^{-1} obtained higher transpiration rates (2.45 and 2.49 mmol H_2O m^{-2} s^{-1}), with increments of 27.60 and 29.68%, respectively, when compared with plants subjected to the same salinity level and not treated with pyruvate. In addition, attenuation of salt stress was recorded at the water salinity level of 2.4 dS m^{-1}, when the plants received pyruvate.

It can also be interpreted that the non-significance of E at the highest dose of pyruvate may be a mitigating effect on plants subjected to high salinity, as it does not increase water loss (E), nor do the stomata close (gs), with benefits for photosynthesis, which was also reflected in the intrinsic water use efficiency (WUEi). The 50 mM dose resulted in a 20.62% increase in transpiration in plants irrigated with the intermediate salinity level (2.4 dS m^{-1}), compared to those that did not receive pyruvate. With its supplementation, plants had greater availability of energy, which must have signaled the regulation of mechanisms of adaptation to salt stress.

Positive effects of pyruvate were also observed in situations of water stress in peanuts. Barbosa et al. (2021) found an attenuation of physiological disturbances caused by water stress, especially at a concentration of 50 mM of pyruvate, with increases of 56% in stomatal conductance, 46% in transpiration and 93% in the CO_2 assimilation rate, compared to plants under stress, without application of pyruvate. For the cv. 'BR1', the positive effect on gas exchange parameters coincided with restoration of the action of antioxidant enzymes, which resulted in an increase in SOD (45%), CAT (129%), and APX (60%) indices. In the literature, it is reported that physiological and biochemical processes in plants are closely related, with effects intrinsically associated in cascades (Pahwa & Ghai, 2015).

According to the summary of analysis of variance (Table 6), there was a significant effect of salt concentration and pyruvate application levels on plant growth (PH, SD, NL, and LA), phytomass (RDM, ShDM, and TDM), and Dickson quality index (DQI). Considering that it is more important to discuss the effects of interaction when significant, there was an interactive effect between the factors (ECw × P) only for RDM.

The increase in the electrical conductivity of the irrigation water (4.0 dS m^{-1}) negatively affected the variables PH, SD, NL, and LA of passion fruit plants, with reductions of 19.76, 5.29, 21.54, and 15.77% respectively, compared to the results obtained in plants subjected to the lowest salinity level (0.8 dS m^{-1}) (Table 7).

The reduction observed in the growth variables due to increase in water salinity can be explained by the osmotic effect to which the plants were exposed, with more pronounced effects on height and leaves. The excess of soluble salts in the soil solution makes the energy state of water more negative, with a reduction in its absorption by the plant, which causes changes in cell metabolism and causes damage to processes related to photosynthesis, cell elongation, and cell wall elasticity throughout plant growth (Ma et al., 2020; Ketehouli et al., 2019).

The plant leaf apparatus is usually the most affected by salt stress, both in number and in area, as leaves are relatively fast growing organs (Ma et al., 2020). These results, in general, corroborate those obtained by Silva Neta et al. (2021), who observed a reduction in LA of 4.67% per unit increase in ECw.

Reductions in the growth of yellow passion fruit seedlings irrigated with saline water were also observed by several authors, such as Oliveira et al. (2015), who found reductions of 37.0, 13.8, and 42.3% for height, stem diameter, and number of leaves (at ECw = 3.5 dS m^{-1}) of yellow passion fruit seedlings, respectively, as well as Bezerra et al. (2016), who also observed harmful effects of salinity on the growth of yellow passion fruit genotypes, and Silva et al. (2021), who observed a reduction of 28.42% in plants irrigated with water of 2.8 dS m^{-1} in the relative growth rate in plant height.

The other factor studied, supplementation with pyruvate, favored plant growth, regardless of the salinity levels of the irrigation water. At the concentration of 50 mM of pyruvate, there was an increase in all the passion fruit growth variables. There were increments of 21.77% in plant height, 12.65% in leaves, and 19.88% in NL. Stem diameter was the variable with the least increase (5.62%), compared to plants that did not receive pyruvate application (Table 7). The concentration of 25 mM of pyruvate was statistically different from the treatment without its application only for the stem diameter.

When analyzing the interaction between irrigation water salinity levels and pyruvate concentrations for RDM (Table 8), it is observed that the application of calcium pyruvate at 25 and 50 mM concentrations were effective in increasing root dry mass at all saline levels of irrigation water. The increase referring to the concentrations of 25 and 50 mM were 23.61 and 58.33% (at EC_w of 0.8 dS m^{-1}), 18.46 and 66.15% (at EC_w of 2.4 dS m^{-1}), and 29.09 and 27.27% (at ECw of 4.0 dS m^{-1}), when compared to plants

Table 6. Summary of the analysis of variance for plant height (PH), stem diameter (SD), number of leaves (NL), leaf area (LA), root dry mass (RDM), shoot dry mass (ShDM), total dry mass (TDM), and Dickson quality index (DQI) of the seedlings of passion fruit cv. Redondo Amarelo cultivated with saline waters and supplementation with calcium pyruvate, 70 days after emergence

Sources of variation	DF	Mean squares							
		PH	SD	NL	LA	RDM	ShDM	TDM	DQI
Blocks	3	12.02^{ns}	0.01^{ns}	1.67^{ns}	4116.29^{ns}	0.00^{ns}	0.24^{ns}	0.25^{ns}	0.00^{ns}
Salinity (ECw)	2	216.84^{*}	0.17^{**}	50.47^{**}	39603^{**}	0.22^{**}	1.95^{*}	3.46^{**}	0.01^{**}
Pyruvate (P)	2	187.21^{*}	0.18^{**}	11.38^{*}	26319.78^{*}	0.33^{**}	7.46^{**}	10.91^{**}	0.03^{**}
ECw × P interaction	4	12.71^{ns}	0.03^{ns}	3.25^{ns}	8014.86^{ns}	0.04^{**}	0.33^{ns}	0.24^{ns}	0.00^{ns}
Residual	24	42.67	0.01	2.74	4993.95	0.00	0.40	0.41	0.00
CV (%)	-	16.88	2.94	10.13	13.94	4.58	15.19	12.83	12.03

CV - Coefficient of variation; DF - Degrees of freedom; ns, *, ** - Not significant, significant at $p \leq 0.05$ and at $p \leq 0.01$ by F test, respectively

Table 7. Means of plant height (PH), stem diameter (SD), number of leaves (NL), and leaf area (LA) of yellow passion fruit plants in seedling stage, under irrigation with saline water and supplementation with calcium pyruvate, 70 days after emergence

Salinity (dS m^{-1})	Means			
	PH (cm)	SD (mm)	NL	LA (cm^2)
0.8	43.00 ± 1.73 a	4.53 ± 4.16 × 10^{-2} a	18.61 ± 0.62 a	572.58 ± 28.89 a
2.4	38.60 ± 1.79 ab	4.39 ± 5.66 × 10^{-2} b	15.83 ± 0.29 b	465.94 ± 16.62 b
4.0	34.50 ± 2.23 b	4.29 ± 4.62 × 10^{-2} b	14.60 ± 0.57 b	482.23 ± 23.06 b
Pyruvate (mM)	**Means**			
0	34.21 ± 1.95 b	4.27 ± 4.70 × 10^{-2} b	15.33 ± 0.95 b	454.65 ± 12.08 b
25	40.21 ± 1.97 ab	4.42 ± 2.69 × 10^{-2} a	16.44 ± 0.53 ab	521.03 ± 30.32 ab
50	41.66 ± 1.99 a	4.51 ± 6.29 × 10^{-2} a	17.27 ± 0.45 a	545.07 ± 27.91 a

In each variable, means with the same letter do not differ from each other by the Tukey test ($p \leq 0.05$)

Table 8. Means of root dry mass (RDM), in yellow passion fruit plants in seedling phase, under irrigation with salinized water and exogenous application of calcium pyruvate, 70 days after emergence

Variable	Salinity ($dS\ m^{-1}$)	Pyruvate (mM)		
		0	25	50
RDM	0.8	$0.72 \pm 1.54 \times 10^{-2}$ cA	$0.89 \pm 2.65 \times 10^{-2}$ bA	$1.14 \pm 3.54 \times 10^{-2}$ aA
	2.4	$0.65 \pm 1.41 \times 10^{-2}$ cB	$0.77 \pm 1.08 \times 10^{-2}$ bB	$1.08 \pm 6.24 \times 10^{-3}$ aA
	4.0	$0.55 \pm 1.63 \times 10^{-2}$ bC	$0.71 \pm 1.43 \times 10^{-2}$ aB	$0.70 \pm 5.55 \times 10^{-4}$ aB

Means with the same lowercase letters between doses of pyruvate do not differ significantly from each other and means with the same uppercase letters between salinity levels do not differ significantly from each other by the Tukey test ($p \leq 0.05$)

that did not receive pyruvate. As a crucial organic compound in the Krebs cycle metabolism, pyruvate attenuated the effects of salt stress on root dry mass, possibly by contributing to the plant's defense system in an environment with salinity problems.

When the plants were subjected to irrigation water salinity and without pyruvate application, a significant difference was observed between the three salinity levels. However, at the 25 mM concentration of pyruvate, the low salinity level (0.8 $dS\ m^{-1}$) produced higher RDM (0.89 g) compared to the 2.4 and 4.0 $dS\ m^{-1}$ levels. Furthermore, the application of 50 mM of pyruvate increased the RDM of passion fruit plants by 62.85 and 54.28% at salinity of 0.8 and 2.4 $dS\ m^{-1}$, respectively, compared to ECw of 4.0 $dS\ m^{-1}$ (Table 8).

The increase in the electrical conductivity of irrigation water (4.0 $dS\ m^{-1}$) negatively affected the ShDM, TDM, and DQI of passion fruit, with reductions of 17.51, 19.18, and 13.51% respectively, compared to the results obtained in plants subjected to the lowest salinity level (0.8 $dS\ m^{-1}$) (Table 9). Different results were found by Lima et al. (2021b) when evaluating the percentage of cell membrane damage, contents of photosynthetic pigments, and growth of sour passion fruit seedlings, cv. BRS RC, under irrigation with saline water and potassium fertilization, as they observed reductions of 57.14 and 35.63% in total dry biomass and Dickson quality index, respectively, compared to the treatment with the lowest salinity level (0.3 $dS\ m^{-1}$).

The DQI indicates the robustness and balance of the biomass distributed in the plant (Dickson et al., 1960). According to Diniz et al. (2020), passion fruit seedlings with a DQI above 0.2 are considered to be of good quality for field establishment. In this study, salinity of up to 4 $dS\ m^{-1}$ did not affect the quality of passion fruit seedlings, with DQI of 0.32 at the highest salinity level (ECw of 4.0 $dS\ m^{-1}$). Similar results to those of the present study were found by Diniz et al. (2020), who subjected passion fruit plants to 3.1 $dS\ m^{-1}$ and obtained seedlings with a DQI of 0.31.

Table 9. Means of shoot dry mass (ShDM), total dry mass (TDM), and Dickson quality index (DQI) of the seedlings of passion fruit cv. Redondo Amarelo cultivated with saline waters and supplementation with calcium pyruvate, 70 days after emergence

Salinity ($dS\ m^{-1}$)	Means		
	ShDM	TDM	DQI
0.8	4.51 ± 0.22 a	5.42 ± 0.26 a	$0.37 \pm 1.61 \times 10^{-2}$ a
2.4	4.29 ± 0.25 ab	5.12 ± 0.29 a	$0.36 \pm 1.76 \times 10^{-2}$ a
4.0	3.72 ± 0.29 b	4.38 ± 0.31 b	$0.32 \pm 1.80 \times 10^{-2}$ b
Pyruvate (mM)	**Means**		
0	3.34 ± 0.16 b	3.98 ± 0.18 b	$0.30 \pm 1.37 \times 10^{-2}$ c
25	4.28 ± 0.26 a	5.07 ± 0.27 a	$0.35 \pm 1.18 \times 10^{-2}$ b
50	4.91 ± 0.17 a	5.88 ± 0.19 a	$0.41 \pm 1.47 \times 10^{-2}$ a

In each variable, means with the same letter do not differ from each other by the Tukey test ($p \leq 0.05$)

However, when analyzing the individual effect of pyruvate, its application increased ShDM by 28.14 and 47.00%, TDM by 27.38 and 47.73% and DQI by 16.66 and 36.66%, respectively, for 25 and 50 mM of pyruvate compared to the treatment without pyruvate (Table 9).

The increase observed in the variables of growth, phytomass and DQI when plants received pyruvate may be related to its beneficial effect. As it is an essential organic compound in cellular respiration, there was possibly greater availability of pyruvate molecules, reinforcing the substrate in the Krebs cycle, for the production of ATP. The effect of calcium pyruvate must have been reinforced by the presence of calcium in its molecule. Hadi & Karimi (2012) mention that calcium is essential in the processes that preserve the structure and functionality of cell membranes, as well as the cell wall structures, besides regulating the transport and selectivity of ions, such as enzymatic activities of the cell wall.

Consequently, the plants were favored in their growth, phytomass and DQI but without an interactive effect with the concentration of salts, that is, pyruvate did not attenuate the effects of salinity on the growth of passion fruit seedlings. Barbosa et al. (2021), in peanut plants of cv. IAC Caiapó (drought-sensitive), found that exogenous application of pyruvate contributed to mitigating the effects of water stress. In the drought-tolerant 'BR 1', pyruvate restored the action of antioxidant enzymes at a concentration of 50 mM.

Conclusions

1. The salinity of irrigation water of 4 $dS\ m^{-1}$ substantially reduces growth, phytomass and Dickson quality index and increases electrolyte leakage in passion fruit seedlings cv. Redondo Amarelo.

2. Exogenous application of calcium pyruvate (25 and 50 mM) favors growth, phytomass, Dickson quality index, relative water content and leaf succulence and reduces electrolyte leakage in the leaf blade in passion fruit.

3. Exogenous application of pyruvate attenuates salt stress, with beneficial effects on CO_2 assimilation rate, transpiration, instantaneous carboxylation efficiency, intrinsic water use efficiency, and root dry mass.

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