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Morphophysiology of yellow passion-fruit seedlings cultivated with macrophyte (*Eichhornia Crassipes*) under salt stress

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ABSTRACT

The use of aquatic macrophyte biomass could be a viable alternative for producing substrates. The objective was to evaluate the production of yellow passion fruit seedlings in different macrophyte-based substrates under salinity stress. The experiment was carried out at the Seedling Production Unit in Redenção, Ceará state. A completely randomized design was used, in a 2 × 5 factorial arrangement, with respect to two electrical conductivities of irrigation water (0.8 and 2.5 dS m^{-1}) and five substrates (S1 = 54% soil + 29. 5% sand + 16% macrophyte; S2 = 34% soil + 33% sand + 33% macrophyte; S3 = 24% soil + 26.5% sand + 49.5% macrophyte; S4 = 20% soil + 14% sand + 66% macrophyte; and S5 = 10% soil + 7.5% sand + 85.5% macrophyte), with 10 replications. Salt stress negatively affected photosynthesis, transpiration, stomatal conductance and internal CO_2 concentration of yellow passion-fruit seedlings. The use of S1 (54% soil + 29.5% sand + 16.5% macrophyte) was more efficient for plant height, leaf area, shoot dry mass, root dry mass, and total dry mass, while S5 (10% soil + 7.5% sand + 82.5% macrophyte) provided higher photosynthesis in yellow passion fruit seedlings. Substrate 1 (54% soil + 29.5% sand + 16.5% macrophyte) and S3 (24% soil + 26.5% sand + 49.5% macrophyte) alleviated salinity stress on Dickson quality index and stem diameter. The use of macrophytes has been shown to be beneficial in the production of passion fruit seedlings, with positive effects on development and gas exchange, and alleviation of salt stress.

Keywords: aquatic plant, *Passiflora edulis*, salinity, substrate.

Morfofisiologia de mudas de maracujazeiro amarelo cultivadas com macrófita (*Eichhornia Crassipes*) sob estresse salino

RESUMO

O uso da biomassa de macrófitas aquáticas pode ser uma alternativa viável para produção de substratos. Objetivou-se avaliar a produção de mudas de maracujazeiro-amarelo em diferentes substratos à base de macrófita, sob estresse salino. O experimento foi realizado na Unidade de produção de Mudas, Redenção, estado do Ceará. O delineamento utilizado foi o inteiramente casualizado, em arranjo fatorial 2 × 5, referente a duas condutividade elétrica da água de irrigação (0,8 e 2,5 dS m^{-1}) e cinco substratos (S1= 54 % solo + 29,5% areia + 16% de Macrófita no substrato; S2= 34 % solo + 33% areia + 33% de Macrófita no substrato,; S3= 24 % solo + 26,5% areia + 49,5% de Macrófita no substrato; S4= 20 % solo + 14% areia + 66% de Macrófita no substrato e S5= 10 % solo + 7,5,5% areia + 85,5% de Macrófita no substrato), com 10 repetições. O estresse salino afetou negativamente a fotossíntese, transpiração, condutância estomática e a concentração interna de CO_2 de mudas de maracujazeiro amarelo. A utilização do S1 (54% de solo + 29,5 de areia + 16,5 de macrófita) foi mais eficiente para a altura de plantas, área foliar, massa seca da parte aérea, da raiz e total, enquanto o S5 (10% de solo + 7,5 de areia + 82,5 de macrófita) proporciona maior fotossíntese de mudas de maracujazeiro amarelo. O substrato 1 (54% de solo + 29,5 de areia + 16,5 de macrófita) e o S3 (24% de solo + 26,5 de areia + 49,5 de macrófita) atenuaram o estresse salino para o índice de qualidade de Dickson e o diâmetro do caule. A utilização de macrófitas revelou-se benéfica na produção de mudas de maracujazeiro, com efeitos positivos no desenvolvimento e nas trocas gasosas, e atenuação do stress salino.

Palavras-chave: planta aquática, *Passiflora edulis*, salinidade, substrato.

1. INTRODUCTION

Passion fruit (*Passiflora edulis*) has become a major crop in Brazil, especially in the Northeast region, which accounts for 70% of national production. Due to the high demand for the fruit and its derivatives, it is increasingly cultivated as a source of income for small and medium-sized farmers (Lima *et al*., 2020; Pinheiro *et al*., 2022).

However, the Northeast region is predominantly arid and semi-arid, characterized by erratic annual rainfall, high temperatures, and low humidity, often leading to water scarcity. In addition, the region often experiences brackish water, which is sometimes the only source of water available for irrigation (Figueiredo *et al*., 2020). The poor quality of water resources progressively increases the levels of ions toxic to plants, such as sodium (Na^+) and chloride (Cl^-), leading to changes in osmotic potential, ionic toxicity, and imbalances in nutrient absorption, which directly affect agricultural production, including seedling quality (Silva Junior *et al*., 2020; Sousa *et al*., 2022).

Considering that passion fruit is propagated by seed, the production of high-quality seedlings is crucial for a plant to reach its maximum production potential. Therefore, it is essential to use a substrate that allows good root development, balanced water retention and a sufficient level of fertility to enable water and nutrient uptake (Mendoça *et al*., 2021). In addition, a high-quality substrate can mitigate the negative effects of salinity on seedling production. Studies focusing on the development of substrates with alternative materials have gained prominence, especially under saline conditions. Sousa *et al*. (2023), using biochar and Lessa *et al*. (2023) evaluating substrates with cattle manure found that these materials provided better quality seedlings even under salinity stress conditions.

In this context, aquatic macrophytes, considered as spontaneous plants or aquatic weeds, have gained attention in recent decades due to their high growth rate, which is directly related to the eutrophication of water bodies. According to Souza *et al*. (2021), the biomass of macrophytes can be used for phytoremediation, fertilizer, biogas, animal feed, aquaculture as food, and wastewater treatment. Thus, the use of macrophytes as organic compounds for substrate production represents a sustainable and economical alternative based on ecological principles, as they are abundantly available in polluted water bodies (Azevedo *et al*., 2022). In addition, promising studies have already demonstrated the ability of macrophytes to release nutrients such as nitrogen, calcium, and magnesium, which may become a trend due to their wide availability (Amatussi *et al*., 2020; Sousa *et al*., 2024). However, little work has been done on substrates formulated with aquatic macrophytes.

Given the above, this study aimed to evaluate the production of yellow passion fruit seedlings in different proportions of substrates based on macrophyte biomass and soil, irrigated with brackish water.

2. MATERIAL AND METHODS

The experiment was conducted in a greenhouse with light interception from August to September 2022 at the Auroras Seedling Production Unit (UPMA), an experimental area belonging to the Universidade da Integração Internacional da Lusofonia Afro-Brasileira (UNILAB), located in the municipality of Redenção, Ceará (4º13'33'' S, 38º43'50'' W, altitude 88.8 m). The climate of the region is classified as BSh', characterized by very high temperatures and precipitation in the summer and autumn (Alvares *et al*., 2013). The climatic data during the study period can be observed in Figure 1.

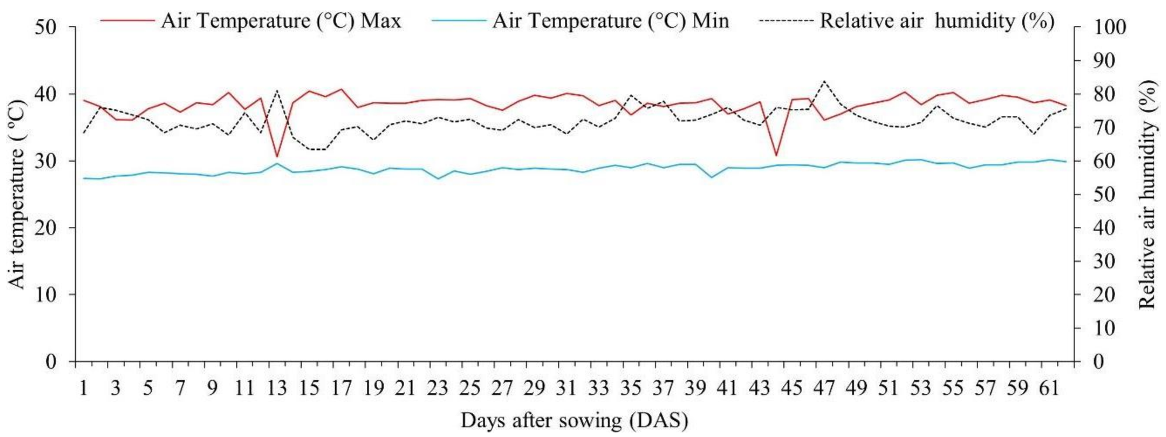

Figure 1. Average values of temperature and relative humidity during the experimental period.

The experimental design used was a completely randomized design in a 2 × 5 factorial arrangement, with reference to two levels of irrigation water electrical conductivity (0.8 dS m^{-1} and 2.5 dS m^{-1}) and five substrate compositions, using different percentages of biomass of the macrophyte species *Eichhornia crassipes* (Mart.) (water hyacinth) and soil, with ten replicates. The compositions of the substrates according to each treatment are shown in Table 1.

The macrophyte used, *Eichhornia crassipes* (Mart.), is an aquatic macrophyte commonly known as water hyacinth, considered one of the main floating aquatic plant species causing environmental problems in various tropical regions due to its rapid and efficient proliferation capacity. It was collected from the Piroás Experimental Farm (PEF) reservoir, which belongs to UNILAB. After collection, the plants were placed in a protected environment for eight days to dehydrate and then ground. The soils used for the composition of the substrates were collected from the experimental area and classified as Ultisol.

Table 1. Composition of substrates used in the experiment.

Substrate	Soil	Sand	Macrophyte
	%		
S1	54	29.5	16.5
S2	34	33	33
S3	24	26.5	49.5
S4	20	14	66
S5	10	7.5	82.5

After preparing the substrates by homogenizing the materials according to the treatment proportions (Table 1), representative samples were collected for chemical analysis as described by Teixeira *et al*. (2017). The characteristics of the substrates are presented in Table 2.

Table 2. Chemical characteristics of the substrates.

Substrates	pH	P	Ca	Mg	Na	K	H+Al	Al	SB	CEC	V	OM	N	ECse
	(water)	mg/kg	cmol$_c$ kg^{-1}								%	g kg^{-1}		dS m^{-1}
S1	5.8	1	1	1.1	0.1	0.24	1.98	0.2	2.4	4.4	55	4.86	0.29	0.29
S2	6.5	9	3.4	1.6	0.2	0.23	4.62	0.25	5.4	8.1	67	17.3	0.47	0.85
S3	6.7	20	6.5	2.3	0.5	0.33	0.99	0	9.6	10.6	91	14.8	0.95	2.44
S4	6.3	31	5.9	4.8	1.2	1.01	1.82	0.5	12.9	14.8	88	25.7	1.67	3.41
S5	6.3	23	5.9	1.1	0.8	0.68	1.82	0.3	8.5	10.3	82	18.2	1.15	3.37

OM - Organic matter; SB - Sum of bases ($Ca^{2+} + Mg^{2+} + Na^{+} + K^{+}$); CEC – Cation exchange capacity - [$Ca^{2+} + Mg^{2+} + Na^{+} + K^{+} + (H^{+} + Al^{3+})$]; V – Base saturation - ($Ca^{2+} + Mg^{2+} + Na^{+} + K^{+}$/ CEC) × 100; ECse – Electrical conductivity of the saturation extract of the substrate; S1 – Soil (54%) + Sand (29.5%) + Macrophyte (16.5%); S2 - Soil (34%) + Sand (33%) + Macrophyte (33%); S3 - Soil (24%) + Sand (26.5%) + Macrophyte (49.5%); S4 - Soil (20%) + Sand (14%) + Macrophyte (66%); S5 - Soil (10%) + Sand (7.5%) + Macrophyte (82.5%).

Topseed® yellow round passion fruit seeds with 75% germination and 99% purity were used. Sowing was done in polyethylene bags of 12 × 20 cm, filled with 1.5 dm³ of the corresponding substrates for each treatment. At 16 days after sowing (DAS), thinning was performed, leaving only the most vigorous plant in each experimental unit.

At the same time (16 DAS), the differentiation of the irrigation treatments began. The fresh water with low salinity (0.8 dS m^{-1}) was taken from the supply system of the unit. The water with higher electrical conductivity (2.8 dS m^{-1}) was prepared by dissolving sodium chloride (NaCl), calcium chloride ($CaCl_2.H_2O$) and magnesium chloride ($MgCl_2.6H_2O$) in the supply water. The amounts were determined to achieve the desired ECw in a ratio of 7:2:1, following the relationship between ECw and concentration (mmol$_c$ L^{-1} ≈ EC × 10) according to Rhoades *et al*. (2000).

Irrigation was performed daily and calculated according to the principle of the drainage lysimeter using the water balance method to keep the substrates at field capacity. A leaching fraction was applied every two days as recommended by Ayers and Westcot (1999). The amount of water applied was determined according to Equation 1.

$$VI = \frac{(Vp - Vd)}{(1 - LF)} \tag{1}$$

Where:

VI - Volume of water to be applied in the irrigation event (mL);

Vp - Volume of water applied in the previous irrigation event (mL);

Vd - Volume of water drained (mL); and,

LF - Leaching fraction of 0.15;

At 62 DAS, the seedlings were ready for transplanting as described by Gontijo (2017), with a height ranging from 15 to 30 centimeters. The biometric variables analyzed were: seedling height (SH, cm), measured from the base of the plant to the last expanded leaf; stem diameter (SD, mm), measured 2 cm above the substrate using a digital caliper with an accuracy of 0.05 mm; number of leaves (NL), determined by direct counting of fully expanded leaves; and leaf area (LA, cm^2), measured using a leaf area meter (LI-3100, Li-Cor, Inc., Lincoln, NE, USA).

Physiological parameters of the seedlings were also measured during this period: CO_2 assimilation rate (A, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (gs, mol m^{-1} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), internal carbon concentration (Ci, μmol CO_2 mol^{-1}), and instantaneous water use efficiency (WUEi - through the ratio between A/E, [(μmol CO_2 m^{-2} s^{-1}) (mol H_2O m^{-2} $s^{-1)-1}$]) using an infrared gas analyzer (IRGA, LI 6400 XT, LICOR). Measurements were made in an open system with an air flow rate of 300 mL min^{-1} between 09:00 and 11:00, under natural air temperature and CO_2 concentration conditions, on fully expanded leaves.

The plants were then removed and separated into different organs (roots, stem, and leaves), then further divided into shoot and root systems. They were placed in labeled paper bags and dried in a forced air circulating oven at 65°C for 48 hours until constant mass was reached, after which the dry mass was weighed using an analytical balance to obtain shoot (SDM), root (RDM), and total dry mass (TDM).

Based on these evaluations, the Dickson Quality Index (DQI) was calculated according to Equation 2 (Dickson *et al*., 1960).

$$DQI = \frac{TDM\ (g)}{\frac{SH(cm)}{SD\ (mm)} + \frac{SDM\ (g)}{RDM\ (g)}} \quad (2)$$

Where:

DQI - Dickson quality index;

TDM - Total dry matter (g per plant);

SH - Seedling height (cm); and,

SD - Stem diameter (mm);

To assess normality, the obtained data were subjected to the Kolmogorov-Smirnov test ($p \leq 0.05$). After verifying normality, the data were subjected to analysis of variance using the F test, and in case of significance, the data were subjected to the Tukey test ($p \leq 0.05$), using the software Assistat 7.7 Beta (Silva and Azevedo, 2016).

3. RESULTS AND DISCUSSION

The results of the analysis of variance (Table 3) indicate that the different proportions of substrate based on water hyacinth biomass and soil exerted an isolated effect on the variables of seedling height ($p > 0.01$). Furthermore, the analysis revealed a significant interaction between water and substrate factors on stem diameter and Dickson Quality Index ($p \leq 0.05$ and $p \leq 0.01$). Additionally, the results indicated that leaf area, shoot dry mass, root dry mass, and total dry mass were affected by the proportions of substrate based on water hyacinth biomass and soil ($p > 0.01$).

Table 3. Summary of the analysis of variance for height (SH), leaf area (LA), stem diameter (SD), shoot dry mass (SDM), root dry mass (RDM), total dry mass (TDM), and Dickson Quality Index (DQI) of yellow passion fruit seedlings subjected to different substrates and salt stress.

Source of variation	DF	Mean square						
		SH	LA	SD	SDM	RDM	TDM	DQI
ECw (E)	1	1.5^{ns}	76^{ns}	0.84^{ns}	0.04^{ns}	0.11^{ns}	0.25^{ns}	0.03^{ns}
Substrates (S)	4	7297.8**	5302**	0.60*	32.53**	2.3**	11.75**	3.68**
E × S	4	125.3^{ns}	620^{ns}	15.74*	0.6^{ns}	0.16^{ns}	0.179^{ns}	2.77**
Residue	40	8451.8	7430	8.11	6.34	1.88	3.3	0.36
Total	49							
CV %	-	23.84	17.92	14.77	27.31	22.23	26.98	23.89

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

In Figure 2A it can be observed that substrate S1 was statistically different from the other substrates for the variable seedling height, showing an increase of 61.80% compared to treatment S3 (which had the lowest performance). This result could be related to the low Na^+ content in S1, which caused less salinity stress to the plants, meaning that it did not affect nitrogen uptake, a fundamental element for seedling growth.

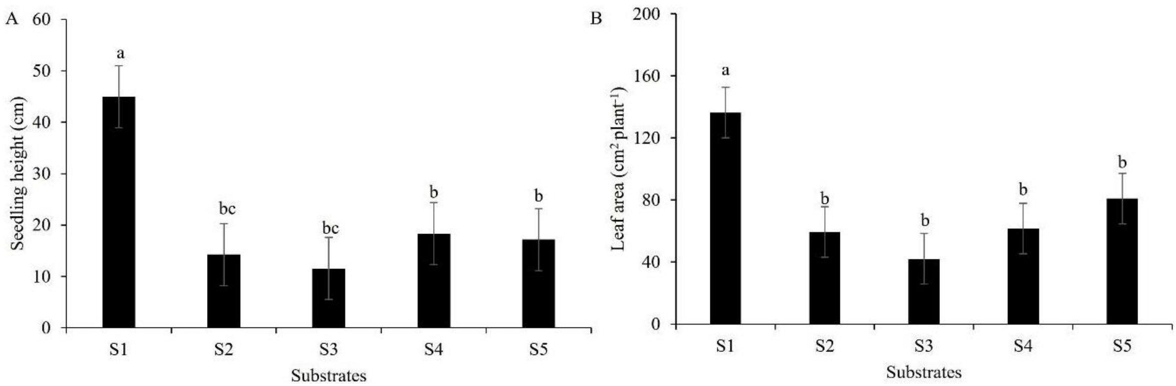

Figure 2. Seedling height (A) and leaf area (B) of yellow passion fruit seedlings grown in different substrates. S1 – Soil (54%) + Sand (29.5%) + Macrophyte (16.5%); S2 - Soil (34%) + Sand (33%) + Macrophyte (33%); S3 - Soil (24%) + Sand (26.5%) + Macrophyte (49.5%); S4 - Soil (20%) + Sand (14%) + Macrophyte (66%); S5 - Soil (10%) + Sand (7.5%) + Macrophyte (82.5%). Lowercase letters compare means by Tukey test ($p \leq 0.05$). Vertical bars are standard errors ($n = 10$).

Similarly, Siqueira *et al.* (2020), who evaluated alternative substrates composed of 50% carbonized rice husk + 50% soil for passion fruit seedling production, found values ranging from 3.9 to 26.7 cm at 60 DAS. Different results were described by Mendonça *et al.* (2021), who evaluated the proportions of carnauba leaves as substrate to produce yellow passion fruit seedlings and obtained better performance in plant height (125 cm) in the composition with a higher proportion of carnauba leaves and soil-based substrate (75% + 25%, respectively).

According to Figure 2B, plants subjected to treatment S1 had a larger leaf area, which was statistically superior to the other substrates. Possibly, the low electrical conductivity of the saturation extract present in this substrate promoted greater leaf expansion in passion fruit seedlings. Passion fruit is considered to be moderately sensitive to salinity in water and soil saturation extract (Ayers and Westcot, 1999). Similar results to the data in this study were reported by Lessa *et al*. (2022) in yellow passion fruit seedlings, where according to these authors, the substrate composed of sand + soil + cattle manure provided a greater leaf area. Similarly, Mendonça *et al*. (2021) found a greater leaf area in yellow passion fruit seedlings with the substrate composed of soil (25%) + carnauba leaves (75%), substrates that presented higher acidity levels, which may have facilitated cation exchange, facilitating nutrient absorption.

When analyzing the results for the stem diameter variable (Figure 3), Substrates 1 and 5, associated with the use of water with lower salinity, stood out statistically. Salt stress, caused by high concentrations of salts in the root zone, interferes with the physiological and metabolic processes of plants through toxic effects of ions and by hindering water absorption by the roots and consequently stem diameter (Taiz *et al*., 2021).

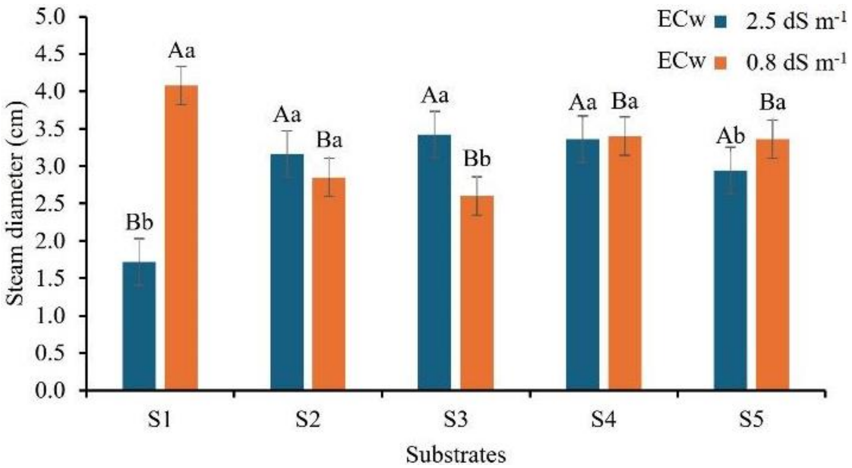

Figure 3. Steam diameter of yellow passion fruit seedlings grown in different substrates under salt stress. S1 – Soil (54%) + Sand (29.5%) + Macrophyte (16.5%); S2 - Soil (34%) + Sand (33%) + Macrophyte (33%); S3 - Soil (24%) + Sand (26.5%) + Macrophyte (49.5%); S4 - Soil (20%) + Sand (14%) + Macrophyte (66%); S5 - Soil (10%) + Sand (7.5%) + Macrophyte (82.5%). Lowercase letters compare means by Tukey test ($p \leq 0.05$). Vertical bars are standard errors (n = 10).

A similar trend was described by Freire and Nascimento (2018), who observed a negative effect of irrigation water salinity on yellow passion fruit seedlings in substrate containing soil + cattle manure. Similar data to S3 were reported by Lessa *et al*. (2023) in yellow passion fruit seedlings irrigated with brackish water. The same authors observed a greater stem diameter in yellow passion fruit seedlings irrigated with water at 3.0 dS m^{-1} when grown in substrates containing charred rice husk.

Regarding the shoot dry mass (Figure 4A), significant differences were found among the evaluated substrates, with seedlings produced in Substrate 1 showing significantly higher mean values compared to the others. This result may be related to the accumulation of different metabolites (solutes) that plants can store in the vacuole of cytoplasmic cells as a strategy to increase their tolerance to water loss induced by salinity stress (Taiz *et al*., 2021).

For the RDM variable (Figure 4B), it is observed that substrates 1, 2, 4 and 5 were not statistically different, being superior to 4. This result may be related to the positive effect of aquatic macrophyte biomass as a substrate, improving the physical and chemical properties of the substrate, favoring the development of seedling root systems, and establishing the presence of beneficial soil microorganisms (Azevedo *et al*., 2022). Similar results were obtained by

Mendonça *et al*. (2021) using a ratio of carnauba straw (75%) + soil (25%) for yellow passion fruit seedlings. A similar trend was observed by Paixão *et al*. (2021), who found an increase in root dry mass values in yellow passion fruit seedlings in substrate containing coffee hulls.

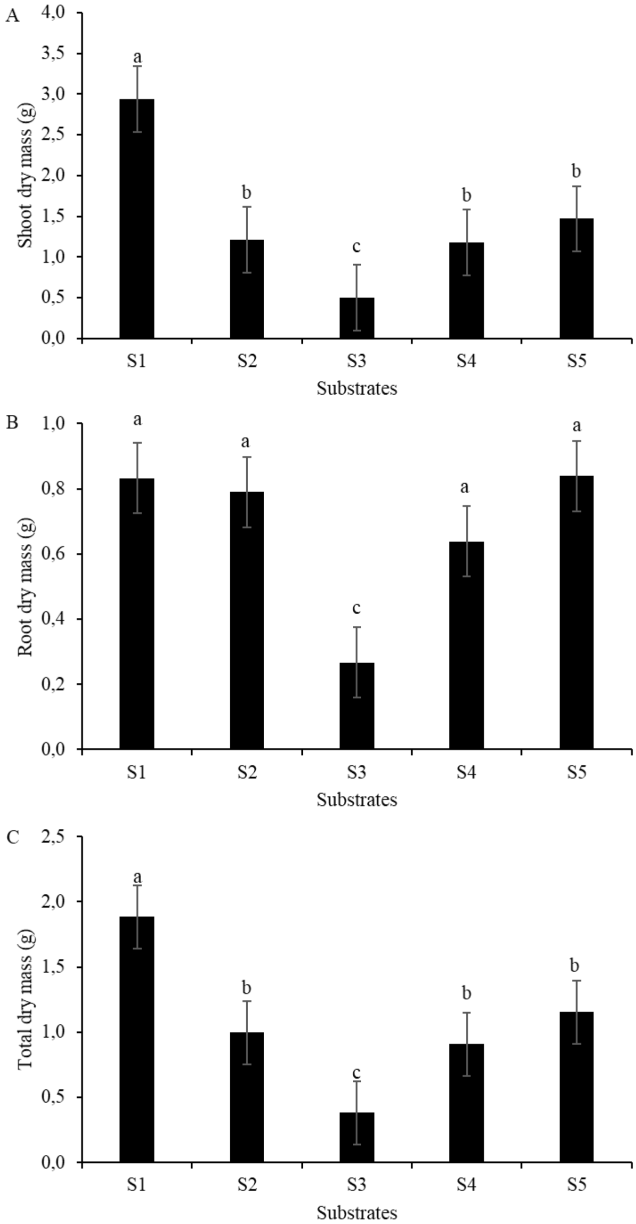

Figure 4. Shoot (A) Root (B) and Total (C) dry mass of yellow passion fruit seedlings grown in different substrates. S1 – Soil (54%) + Sand (29.5%) + Macrophyte (16.5%); S2 - Soil (34%) + Sand (33%) + Macrophyte (33%); S3 - Soil (24%) + Sand (26.5%) + Macrophyte (49.5%); S4 - Soil (20%) + Sand (14%) + Macrophyte (66%); S5 - Soil (10%) + Sand (7.5%) + Macrophyte (82.5%). Lowercase letters compare means by Tukey test ($p \leq 0.05$). Vertical bars are standard errors (n = 10).

Seedlings exposed to substrate S1 presented a statistically superior total dry mass compared to the others (Figure 4C). This result can be explained by the greater supply of available nutrients, without or with the interference of compounds harmful to their absorption, resulting in a greater total biomass. Mendonça *et al*. (2021) also verified the positive effect of the alternative substrate carnauba straw on yellow passion fruit seedlings.

The Dickson Quality Index (Figure 5) presented that under higher salinity conditions (2.5 dS m^{-1}) associated with substrate S5, seedlings obtained higher quality. Under low salinity conditions, S1 was statistically superior to the others. The use of organic/vegetable materials in the composition of the substrates aims at obtaining seedlings of better quality and satisfactory vigor. Thus, it can be observed that the use of macrophyte (S5 = 82.5%) becomes an alternative to compose the substrate for seedling production under higher salinity. Possibly, this result can be related to the proportional increase of macrophyte to its adsorption capacity, causing plants to minimize sodium absorption through transient binding with Na^+, reducing the adverse effects caused by osmotic stress (Sousa *et al*., 2023).

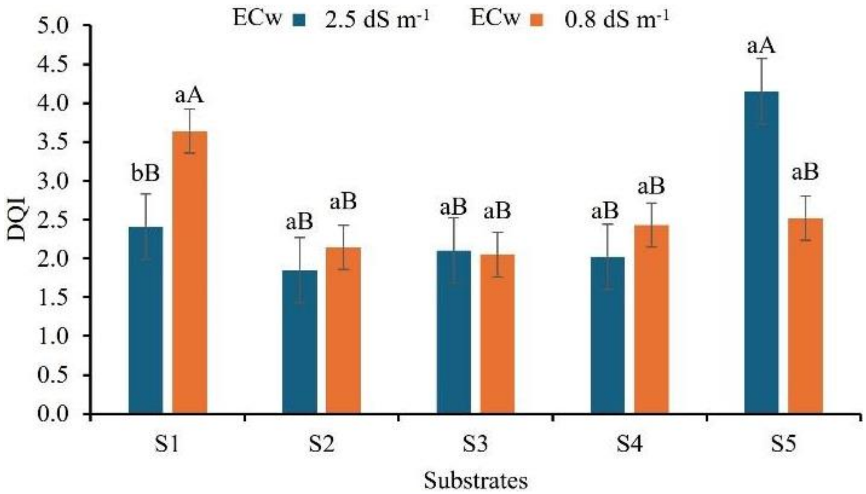

Figure 5. Dickson quality index of yellow passion fruit seedlings grown in different substrates under salt stress. S1 – Soil (54%) + Sand (29.5%) + Macrophyte (16.5%); S2 - Soil (34%) + Sand (33%) + Macrophyte (33%); S3 - Soil (24%) + Sand (26.5%) + Macrophyte (49.5%); S4 - Soil (20%) + Sand (14%) + Macrophyte (66%); S5 - Soil (10%) + Sand (7.5%) + Macrophyte (82.5%). Lowercase letters compare means by Tukey test ($p \leq 0.05$). Vertical bars are standard errors (n = 10).

Evaluating the use of organic matter in the production of yellow passion fruit seedlings under salt stress, Lessa *et al*. (2023) observed higher seedling quality under salinity stress when exposed to a higher percentage of organic matter. Similarly, Almeida *et al*. (2020) observed similar results in *Handroanthus impetiginosus* seedlings, where the substrate with organic compounds irrigated with low salinity water showed the highest IQD. Melo Filho *et al*. (2017) found a decrease in the IQD of pitombeira (*Talisia Esculenta*) seedlings due to an increase in the salinity of the irrigation water.

According to Table 4, there was an isolated effect of irrigation water on photosynthesis, transpiration, stomatal conductance, and internal CO_2 concentration at the significance level ($p \leq 0.01$) and of substrate on photosynthesis and internal CO_2 concentration at the significance level ($p \leq 0.05$).

According to Figure 6A, Substrates 3 and 5 were statistically superior to the others in CO_2 assimilation rate. These results suggest that these fractions may have induced more efficient CO_2 assimilation. The effect of these treatments may be related to the amounts of nitrogen, phosphorus, and potassium present in them (Table 2), because nitrogen serves as a constituent of many plant cell components, including chlorophyll; phosphorus stimulates enzyme activity and RuBisCO synthesis, which favors CO_2 assimilation, which enhances photosynthesis; and potassium regulates stomatal opening (Taiz *et al*., 2021).

Table 4. Summary of the analysis of variance for rates of CO_2 assimilation (A), transpiration (E), stomatal conductance (gs), and internal carbon concentration (Ci), of yellow passion fruit seedlings subjected to different substrates and saline stress.

Source of variation	DF	Mean square				
		A	E	gs	Ci	WUEi
ECw (E)	1	19.12**	19.25**	0.046**	6042**	5.74**
Substrates (S)	4	76*	2.88^{ns}	0.008^{ns}	1557*	0.97**
E × S	4	9.89^{ns}	2.53^{ns}	0.009^{ns}	3588^{ns}	0.51^{ns}
Residue	40	180.66	21.4	0.057	1572	0.20
Total	49					
CV%	-	12.54	25.20	20.14	12.10	18.56

DF – Degrees of freedom; CV – Coefficient of variation; *, **, ns - Significant at p ≤ 0.05 and p ≤ 0.01, and not significant, respectively, by F test.

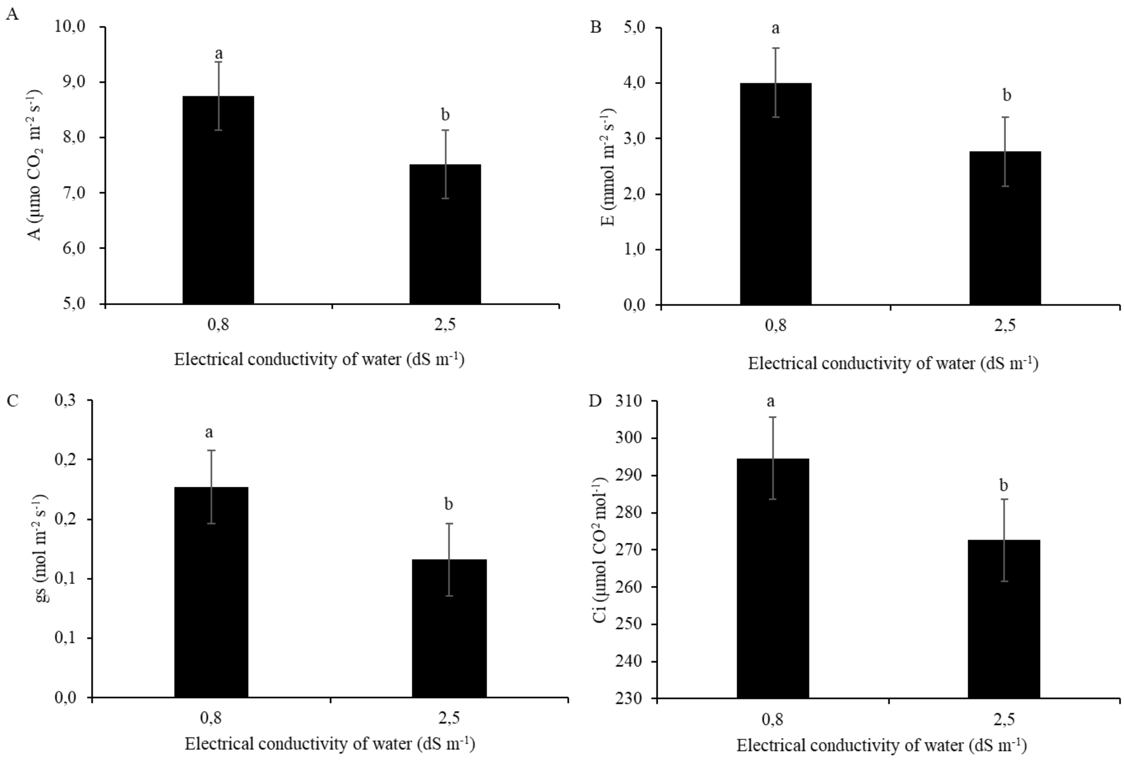

Figure 6. CO2 assimilation rate (A), transpiration (B), stomatal conductance (C), and internal carbon concentration (D) of yellow passion fruit seedlings grown under salt stress. Lowercase letters compare means by Tukey test (p ≤ 0.05). Vertical bars are standard errors (n = 10).

Similar trends to this study were observed by Mendonça et al. (2021) in yellow passion fruit seedlings grown in a substrate with soil (25%) + carnauba bagasse (75%). Results that corroborate with this study were reported by Figueiredo *et al*. (2020), who found a higher photosynthetic rate in passion fruit seedlings grown in a substrate composed of 85% soil, 10% fine sand and 5% cured cattle manure.

Results consistent responses to the reduction in plant photosynthesis with increasing irrigation water salinity were observed by Lima *et al*. (2020), who investigated the effects of NaCl salinity (0 and 150 mM) in three different passion fruit genotypes. They also found a reduction in assimilation rate for all genotypes studied when irrigated with 150 mM.

Transpiration values of yellow passion fruit seedlings were reduced by 31% under irrigation with 2.5 dS m^{-1} water (Figure 6B) compared to the control treatment. The reduction in transpiration in plants under salt stress is due to the osmotic effect of salts, which reduces stomatal conductance to regulate the amount of water absorbed by the roots as a response mechanism aimed at reducing water loss to the atmosphere (Taiz *et al*., 2021). Similarly, Lessa *et al*. (2022) observed that passion fruit seedlings irrigated with 0.3 dS m^{-1} water had the highest transpiration values, statistically different from the 3.0 dS m^{-1} water.

According to Figure 6C, conductance decreased by 34.4% from the highest to the lowest salinity level. The regulation of stomatal aperture is directly influenced by soil water availability, with high osmotic potential conditions leading to a restriction of water uptake by roots, resulting in a decrease in conductance as plant stomata close (Sousa *et al*., 2023). It is also worth noting that partial stomatal closure restricts the entry of CO_2 into leaf mesophyll cells, which can increase susceptibility to photochemical damage by causing excessive light energy in photosystem II (Munns and Tester, 2008).

Similarly, Lessa *et al*. (2023) recorded a decrease in stomatal conductance in yellow passion fruit seedlings irrigated under salt stress. Silva *et al*. (2019), who irrigated yellow passion fruit seedlings with brackish water, also found a reduction in stomatal conductance.

Salt stress negatively affected the internal CO_2 concentration in yellow passion fruit seedlings compared to the control treatment (Figure 6D). With greater stomatal aperture, as demonstrated in this study, plants tend to increase the uptake of atmospheric CO_2 and concentrate it in their tissues (Taiz *et al*., 2021).

In contrast to this study, Lima *et al*. (2020), who studied gas exchange in passion fruit seedlings grown with saline water, observed a decrease in internal CO_2 concentration with increasing ECw. Similarly, Silva *et al*. (2019) also found a decrease in internal CO_2 concentration when comparing higher and lower salinity waters (0.7 and 2.8 dS m^{-1}, respectively).

According to Figure 7A, Substrates 1 and 5 were statistically superior to the others for CO_2 assimilation rate. The effect of these treatments may be related to the amounts of nitrogen, phosphorus, and potassium present in them (Table 2), since N serves as a constituent of many plant cell components, including chlorophyll; phosphorus stimulates enzyme activity and RuBisCO synthesis, which favors CO_2 assimilation and promotes photosynthesis; and K regulates stomatal opening (Taiz *et al*., 2021).

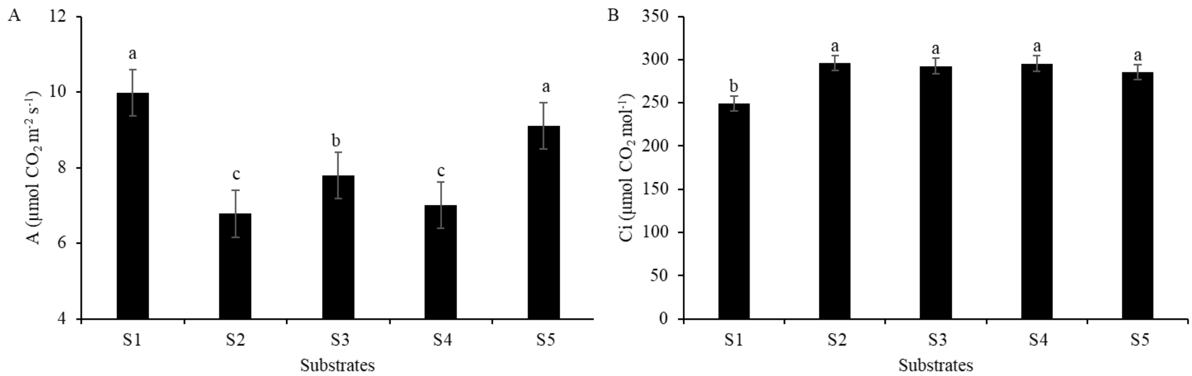

Figure 7. CO2 assimilation rate (A), and internal carbon concentration (B) of yellow passion fruit seedlings grown in different substrates. S1 – Soil (54%) + Sand (29.5%) + Macrophyte (16.5%); S2 - Soil (34%) + Sand (33%) + Macrophyte (33%); S3 - Soil (24%) + Sand (26.5%) + Macrophyte (49.5%); S4 - Soil (20%) + Sand (14%) + Macrophyte (66%); S5 - Soil (10%) + Sand (7.5%) + Macrophyte (82.5%). Lowercase letters compare means by Tukey test ($p \leq 0.05$). Vertical bars are standard errors (n = 10).

Similar trends for higher photosynthetic rates were observed by Mendonça *et al*. (2021) in yellow passion fruit seedlings grown in a substrate of 25% soil + 75% carnauba bagasse, and by Figueiredo *et al*. (2020) in passion fruit seedlings in a substrate composed of 85% soil, 10% fine sand, and 5% cattle manure.

Substrate S1 provided the lowest internal CO_2 concentration for passion fruit seedlings, a result that was statistically different from the other substrates, which did not differ significantly among themselves (Figure 6B). This substrate had a higher amount of soil in its composition compared to the other treatments, and thus a lower amount of macrophytes. The behavior of internal CO_2 concentration as a function of substrate appears to be inversely proportional to that of photosynthesis, explaining that the higher internal carbon consumption in S3 was effective on the net photosynthetic rate through carbon assimilation (Silva *et al*., 2019; Taiz *et al*., 2021).

An increase in ECw from 0.8 to 2.5 dS m^{-1} negatively affected the water use efficiency of passion fruit seedlings, reducing it by 24.6% compared to the lowest salinity level used (Figure 8A).

Under conditions of higher electrical conductivity of the water, a significant accumulation of salts may have occurred, leading to a reduction in the osmotic potential of the solution and consequently a reduction in water uptake by the roots. This leads to lower efficiencies due to reduced stomatal aperture, which reduces CO_2 uptake from the environment and the rate of photosynthesis in these treatments, implying less efficient water use under stress (Taiz *et al*., 2021; Lessa *et al*., 2023).

Lessa *et al*. (2023) found a reduction in the instantaneous water-use efficiency in passion fruit crops with an increase in the electrical conductivity of the irrigation water to which the plants were exposed. Similarly, Pinheiro *et al*. (2022) observed reductions in water use efficiency in passion fruit plants under salinity stress.

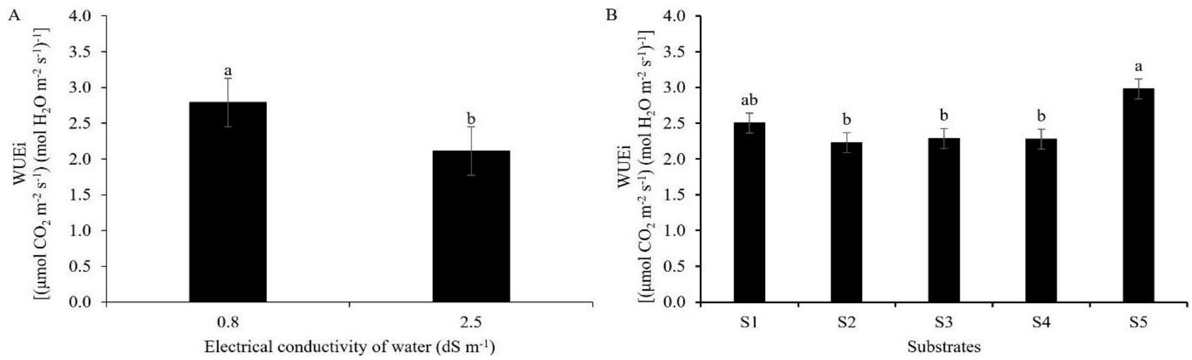

Figure 8. Water-use efficiency of yellow passion fruit seedlings under salt stress (A) and grown in different substrates (B). S1 – Soil (54%) + Sand (29.5%) + Macrophyte (16.5%); S2 - Soil (34%) + Sand (33%) + Macrophyte (33%); S3 - Soil (24%) + Sand (26.5%) + Macrophyte (49.5%); S4 - Soil (20%) + Sand (14%) + Macrophyte (66%); S5 - Soil (10%) + Sand (7.5%) + Macrophyte (82.5%). Lowercase letters compare means by Tukey test ($p \leq 0.05$). Vertical bars are standard errors (n = 10).

It was observed that S5 (10% soil, 7.5% sand, 82.5% macrophyte) provided the highest water use efficiency WUEi (2.98 μmol CO_2 m^{-2} s^{-1}(μmol m^{-2} s^{-1})$^{-1}$), which was statistically different from the others (S2, S3, S4), but showed no significant difference compared to S1 (54% soil, 29.5% sand, 16.5% macrophyte) (Figure 8B).

The higher percentage of sand and macrophyte in Substrates S1 and S5, respectively (Table 1), may have helped to maintain the salt balance in the substrates, preventing salt accumulation from negatively affecting the physiological parameters of the seedlings under these conditions, as observed in the photosynthesis results of this study (Figure 7A). In addition, the water-holding capacity of the substrate and its higher drainage capacity may have facilitated salt leaching (Silva Junior *et al*., 2020).

Therefore, the results suggest that the use of a macrophyte-based substrate under salinity stress likely resulted in increased salt leaching due to the amount of irrigation applied, thus providing better developmental conditions. Thus, determining the optimal substrate composition is crucial for proper seedling development and, consequently, for achieving higher yields and economic returns.

4. CONCLUSIONS

Salt stress negatively affects the morphophysiological characteristics of passion fruit seedlings. These effects include reductions in photosynthesis, transpiration, stomatal conductance, internal CO_2 concentration, and water use efficiency.

The S1 substrate (54% soil, 29.5% sand, 16.5% macrophyte) was most efficient for seedling height, leaf area, and dry mass (shoot, root, and total) while S5 (10% soil, 7.5% sand, 82.5% macrophyte) supported higher photosynthesis and water use efficiency in yellow passion fruit seedlings.

S1 (54% soil, 29.5% sand, 16.5% macrophyte) and S3 (24% soil, 26.5% sand, 49.5% macrophyte) alleviated salt stress, improving Dickson quality index and stem diameter.

The use of macrophytes has been shown to be beneficial in the production of passion fruit seedlings, with positive effects on development and gas exchange, and alleviation of salt stress. Further research is needed to better understand substrate production from macrophyte biomass, including its dynamics and optimal proportions across different environmental settings.

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