

Article

Saline Water Stress in Caatinga Species with Potential for Reforestation in the Face of Advancing Desertification in the Brazilian Semiarid Region

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Abstract

The advance of the soil desertification process and water salinisation hinders reforestation actions in the Brazilian semiarid region due to the negative effects on the initial establishment of seedlings. Knowledge of potential species for overcoming the problems of soil and water salinity is of broad interest. This study evaluated the growth of seedlings of the species *Handroanthus impetiginosus* and *Handroanthus spongiosus* subjected to the combined stresses of salinity and water deficit. The species were subjected to three water depths (WDs): WD1—50%, WD2—75% and WD3—100% of reference evapotranspiration, and four salinity levels (SL): SL1—0.27 dS m^{−1}, SL2—2.52 dS m^{−1}, SL3—6.35 dS m^{−1} and SL4—7.38 dS m^{−1}. Biometric data, including plant height, number of leaves, collar diameter and biomass, was obtained. The results showed that *H. impetiginosus* was more tolerant of the conditions analysed. The species showed greater sensitivity to salt stress, which reduced growth and dry biomass accumulation by up to 98%. Increased water deficit reduced height, collar diameter, number of leaves, root biomass and total biomass. We propose that the optimal water depth for both species is 100% of the reference evapotranspiration.

Keywords: saline stress; water deficit; tolerance; irrigation

1. Introduction

The Caatinga is the largest tropical dry forest in South America and encompasses significant biodiversity, playing an essential role in ecosystem services, providing primary production and nutrient cycling, and mitigating the effects of climate change [1]. However, anthropogenic pressure has intensified the degradation of the Caatinga's native vegetation cover and soil salinisation [2]. It is estimated that approximately 38% of the Caatinga's original vegetation has already been altered to some degree [3]. The loss of original cover is mainly the result of agricultural expansion and frequent logging [4]. These factors, together with the characteristics of the semiarid region, aggravate the process of desertification in the soil and water salinisation, damaging physiological processes such as net photosynthesis, transpiration and CO₂ accumulation in plants [5].

The excess of salts lowers the water potential of the soil, making it difficult for plant roots to absorb water, which impairs nutrition and damages the organelles of the plant cell [6]. When exposed in large quantities, it causes toxicity and makes it difficult to carry out photobiochemical processes [7]. Under these stressful conditions, initial plant growth (e.g., collar diameter, height and biomass accumulation) is negatively affected, as seen in the works by [8,9]. This reduction can be explained by the effect of plasmolysis and/or the nutritional disturbance caused by salts such as sodium (Na⁺) and chloride (Cl⁻) [10,11]. Similarly, water stress causes stomatal closure, reduces water loss to the atmosphere and limits transpiration and CO₂ assimilation, with consequent reductions in photosynthesis [12,13]. In addition to causing a reduction in osmotic potential and water absorption due to the accumulation of solutes [14], water stress can cause plant death depending on the severity of the damage.

Although the effects of combined water and salt stress damage on various agricultural plant species are known, there are doubts about these factors in Caatinga species. Some studies have evaluated the isolated effects of water and salt stress on Caatinga species [2,15,16], but the combined effects of these factors are not well understood and are dependent on the intensity and period of application [17,18]. Understanding these relationships allows for the selection of more adapted individuals, providing a database on the development needs of native Caatinga species.

Species of the genus *Handroanthus* are frequently used in land restoration and urban landscaping projects due to their showy flowers; however, they exhibit low seed viability [19,20]. More specifically, the *Handroanthus impetiginosus* (Mart. ex DC.) Mattos has adaptive characteristics that facilitate its development in stressful environments, which highlights its importance in reforestation projects [21]. It is a perennial species with anemochorous dispersal, a wide geographical distribution and intermediate genetic diversity [22]. However, for species such as *Handroanthus spongiosus* (Rizzini) S.O. Grose, which is endemic to the Caatinga biome and classified as endangered [23], there is a lack of studies and limited information on its ecological and physiological responses to abiotic conditions, hampering its management and conservation. Therefore, this study aimed to investigate the effects of the interaction between salinity and water deficit on the morphological responses of *H. impetiginosus* and *H. spongiosus*.

2. Materials and Methods

2.1. Study Area

Two independent experiments were conducted simultaneously between July 10 and November 20 at the Academic Unit of Serra Talhada, Federal Rural University of Pernambuco, located in the municipality of Serra Talhada, Pernambuco, Brazil (Figure 1). The semiarid region has a BSh climate [24], which according to the Köppen classification is characterised by high temperatures of around 26 °C, intense periods of drought, irregular

rainfall with an annual average of 642 mm year^{-1} , relative humidity close to 63% and a high evapotranspiration rate ($>1600 \text{ mm year}^{-1}$) [25].

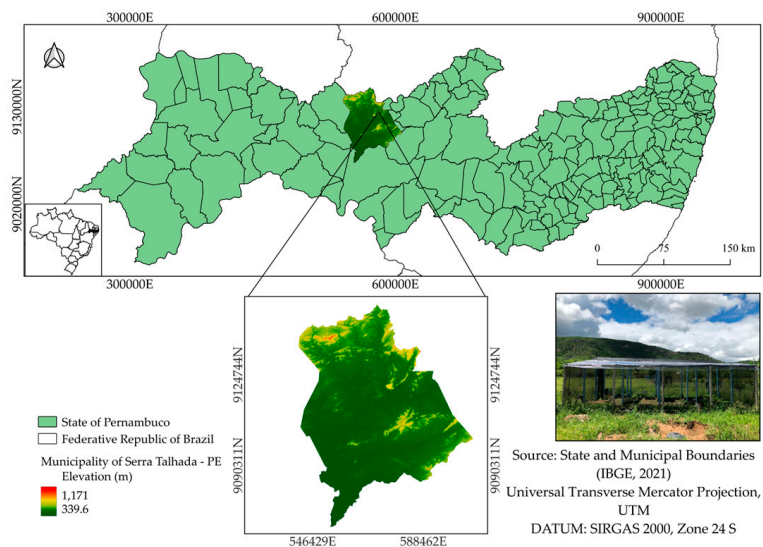


Figure 1. Location of the experimental locale in the municipality of Serra Talhada-PE, Brazil.

2.2. Meteorological Variables

The meteorological variables were monitored from an automatic weather station belonging to the National Institute of Meteorology (INMET) located about 300 m from the experimental nursery. Information was obtained on average air temperature (T — $^{\circ}\text{C}$), relative humidity (RH —%), global solar radiation (R_g — $\text{MJ m}^{-2} \text{ day}^{-1}$) and rainfall (R — mm day^{-1}). During this period, there was an increase in temperatures associated with a reduction in air humidity, a phenomenon characteristic of this time of year. In addition, the rainfall recorded during the experimental period was low (38.60 mm), since the rainy season in the region is concentrated between the months of January and July (Figure 2).

The experiment was carried out in a nursery measuring $4 \times 6 \times 2.8 \text{ m}$, covered with a shading mesh that intercepts 70% of the sun's radiation. It was covered with transparent plastic with a transmissivity of 98% to prevent water from entering as a result of rainfall. The species studied were *H. impetiginosus* and *H. spongiosus*, the seeds of which were acquired through a donation from the Environmental Monitoring Centre (NEMA/UNIVASF). They were sown in Styrofoam trays containing 200 cells and filled with soil with the following characteristics: soil density (1.30 kg dm^{-3}), particle density (2.5 kg dm^{-3}), total porosity (43.3%), sand (815.2 g kg^{-1}), silt (128.4 g kg^{-1}) and clay (56.4 g kg^{-1}), as described by Siqueira et al. [26]; the soil was mixed with homogenised sand at a 2:1 ratio. At this stage, the species received daily water replenishments to avoid water stress. After 78 days of emergence, the seedlings were transplanted into polyethylene bags with a capacity of 8 kg ($31 \times 4 \times 20.5 \text{ cm}$), which were filled with the same substrate. The soil used in the experiment was classified as Typic Eutric Haplic Cambisol, according to protocols by Santos et al. [27], sieved through a 2 mm mesh.

The plants were arranged in a completely randomised design with four replicates. The *H. impetiginosus* and *H. spongiosus* species were subjected to three water depths (WDs) based on reference evapotranspiration (ET_0), where $\text{WD1} = 50\%$, $\text{WD2} = 75\%$ and $\text{WD3} = 100\%$ of ET_0 . To determine ET_0 , the Penman–Monteith method was used, parameterised by the FAO-56 bulletin [28], taking into account the attenuation of radiation resulting from the use of the shading screen.

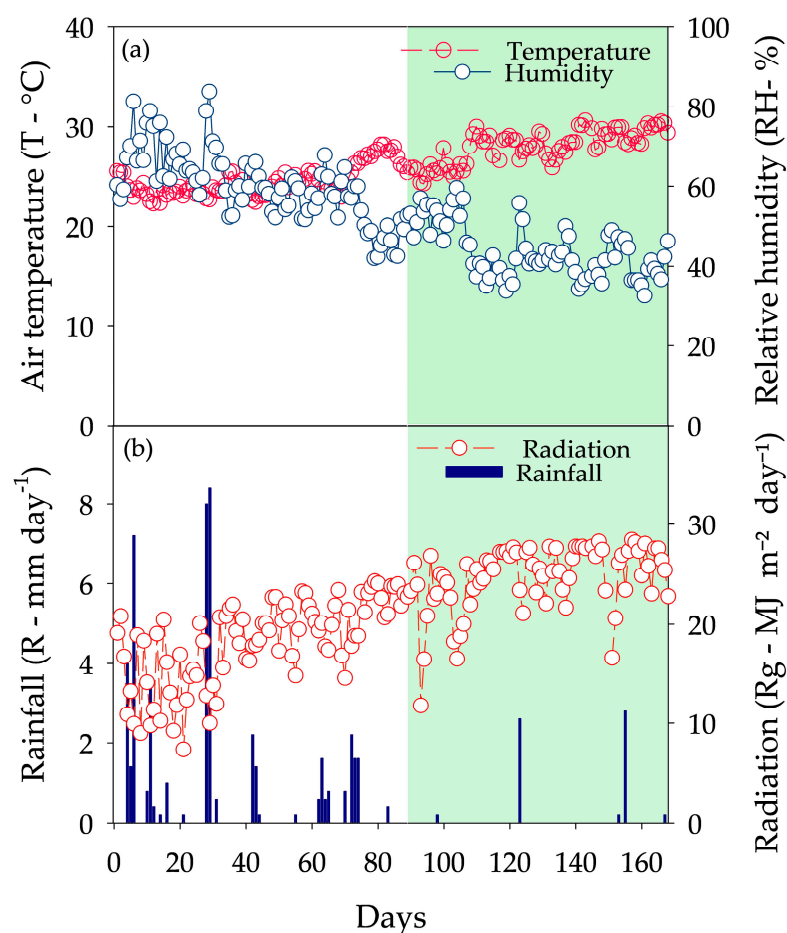


Figure 2. Daily average of meteorological variables: (a) average air temperature (T — $^{\circ}\text{C}$) and humidity (RH, %), (b) global solar radiation (R_g — $\text{MJ m}^{-2} \text{ day}^{-1}$) and rainfall (R — mm day^{-1}) from September 2023, Serra Talhada-PE, Brazil. The period of application of the treatments is represented by the green shade.

In both experiments, the species were subjected to four levels of salinity (SL), SL1— 0.28 dS m^{-1} (control), SL2— 2.52 dS m^{-1} , SL3— 6.35 dS m^{-1} and SL4— 7.38 dS m^{-1} . The saline solution was prepared with analytical-grade NaCl, and the amount to be applied was determined using the equations $\text{TDS} = \text{ECw} \times 640$ and $\text{TDS} = \text{ECw} \times 800$, where TDS represents total dissolved solids, ECw is the electrical conductivity of the water, and 640 and 800 are constants from [29]. Thus, combining the species with the water depths (WDs) and salinity levels (SL), a total of 24 treatments were applied.

Biometric data (i.e., height, collar diameter, number of leaves) and survival data were obtained at 15-day intervals. These data were related to the species' thermal requirements, which were determined using air temperature data [30]. At the end of the experiments, the plants were collected and subdivided into leaves, stem and root and placed in paper bags. They were then taken to a forced ventilation oven for 72 h at 55°C to determine their dry biomass. From this data, the variables dry leaf biomass (DLB), dry stem biomass (DSB), dry root biomass (DRB) and total plant dry biomass ($\text{TDB} = \text{DLB} + \text{DSB} + \text{DRB}$) were obtained. The TDB data was related to the volume of water replenished throughout the cycle to determine the water use efficiency (WUE) using Equation (1) [31]:

$$\text{WUE} = \frac{\text{TDB}}{\text{D}} \quad (1)$$

where TDB is the accumulated total dry biomass of the plant (g) and D is the depth of water applied (L).

2.3. Bioclimatic Variables

2.3.1. Accumulated Degree Days

The micrometeorological data was used to calculate the degree days for the period from 10 July 2023 to 20 September 2023. In this study, we used Equation (2) of Arnold's method 1959 [32]:

$$ADD = \sum_{i=1}^n (T - T_b) \quad (2)$$

where ADD is the accumulated degree days ($^{\circ}\text{C day}$), T is the average temperature ($^{\circ}\text{C}$), T_b is the lower basal temperature (10°C), and n is the number of total days.

2.3.2. Leaf Emergence Rate

The leaf emergence rate (LER) represents the number of days required for a leaf to emerge [33], which was calculated according to the following Equation (3):

$$LER = \frac{NL}{ADD} \quad (3)$$

where NL is the number of fully expanded leaves.

2.3.3. Phyllochron

The phyllochron is defined as the period between leaf emergence on the main stem, and its unit of time is the thermal sum, mainly due to the influence of air temperature on plant development [34,35]. For this specific case, the phyllochron was determined by inverting the rate of leaf emergence ($\text{Phyllochron} = \text{LER}^{-1}$) and was determined only for the treatment in which the best growth was observed.

2.4. Statistical Analysis

All statistical analyses were carried out using R software version 4.4.3. Before the analysis of variance (ANOVA), the data was subjected to normality and homoscedasticity tests, verified by the Shapiro–Wilk and Levene tests. The results of the water depths were compared using Tukey's test at a 5% significance level. Comparisons between salinity levels were made using regression analysis.

3. Results

According to the analysis of variance, the salinity levels (SL) $\times$ species (SPE) were significant for all the variables analysed ($p < 0.05$), showing that the increase in salinity affected the species in different ways (Table 1). On the other hand, the irrigation water depth had no significant impact on dry leaf biomass (DLB), dry stem biomass (DSB) and the diameter/height ratio (CD/PH), suggesting that water limitation was not a determining factor for these variables. Likewise, the interaction between salinity levels $\times$ water depths for dry stem biomass (DSB) and diameter/height ratio (CD/PH).

The triple interaction resulting from the combination of RH, SL and SPE (Table 2) resulted in a significant improvement in the DLB, DRB, TDB and WUE variables for the *H. impetiginosus* species under the WD of 100% ETo and in the salinity control treatment, leading to an accumulation of 52% of dry mass compared to the WD of 75% ETo at the same salinity level. It was observed that as electrical conductivity increased, water use efficiency decreased. This response was also seen as the irrigation depth decreased, so as

the salt concentration increased and the irrigation depth decreased, the variables showed lower results than the 100% depth in the control treatment.

Table 1. Analysis of variance, *p*-value obtained from the analysis of variance for height (PH), diameter (CD), number of leaves (NL), dry leaf biomass (DLB), dry stem biomass (DSB), dry root biomass (DRB), total dry biomass (TDB) and diameter/height ratio (CD/PH), for the species *H. impetiginosus* and *H. spongiosus*, subjected to water depths (WDs) of 50%, 75%, 100% ETo and salinity levels (SL) of 0.27, 2.52, 6.35, 7.38 dS m^{−1}, in Serra Talhada-PE, Brazil.

Factor	PH	CD	NL	DLB	DSB	DRB	TDB	CD/PH
SL	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *
WD	0.003 *	0.006 *	0.000 *	0.109	0.094	0.000 *	0.000 *	0.399
SPE	0.000 *	0.000 *	0.004 *	0.000 *	0.000 *	0.000 *	0.000 *	0.000 *
SL×WD	0.002 *	0.000 *	0.000 *	0.014 *	0.092	0.000 *	0.000 *	0.158
SL×SPE	0.000 *	0.000 *	0.000 *	0.001 *	0.000 *	0.000 *	0.000 *	0.000 *
WD×SPE	0.032 *	0.044 *	0.23	0.004 *	0.484	0.000 *	0.000 *	0.116
SL×WD×SPE	0.179	0.372	0.325	0.008 *	0.09	0.032 *	0.007 *	0.617

The asterisk (*) indicates the significance of the difference between means of the respective variable.

Table 2. Effects of water depths (50%, 75% and 100% ETo), salinity levels (SL1 = 0.278 dS m^{−1}, SL2 = 2.252 dS m^{−1}, SL3 = 6.35 dS m^{−1} and SL4 = 7.38 dS m^{−1}) and species *H. impetiginosus* and *H. spongiosus* in dry leaf biomass (DLB—g), dry root biomass (DRB—g), total dry biomass (TDB—g) and water use efficiency (WUE—g L^{−1}).

Salinity Levels (dS m ^{−1})	Water Depth (%)	Species	DLB (g)	DRB (g)	TDB (g)	WUE (g L ^{−1})
0.28	50	<i>H. impetiginosus</i>	0.73 ^{bcd}	1.68 ^{cde}	2.87 ^{bc}	0.77 ^b
		<i>H. spongiosus</i>	0.40 ^{cde}	0.74 ^{defg}	1.39 ^{cde}	0.37 ^{de}
	75	<i>H. impetiginosus</i>	0.87 ^{bc}	2.13 ^{bc}	3.51 ^b	0.75 ^b
		<i>H. spongiosus</i>	1.16 ^{ab}	2.05 ^{bcd}	3.44 ^b	0.73 ^b
	100	<i>H. impetiginosus</i>	1.63 ^a	4.27 ^a	6.44 ^a	1.13 ^a
		<i>H. spongiosus</i>	0.56 ^{bcd}	1.90 ^{cde}	2.79 ^{bc}	0.49 ^{bcd}
2.25	50	<i>H. impetiginosus</i>	0.63 ^{bcde}	1.52 ^{cdef}	2.63 ^{bcd}	0.70 ^{bc}
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
	75	<i>H. impetiginosus</i>	0.41 ^{cde}	1.62 ^{cde}	2.35 ^{bcd}	0.50 ^{bcd}
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
	100	<i>H. impetiginosus</i>	0.63 ^{bcde}	3.04 ^{ab}	4.04 ^b	0.71 ^{bc}
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
6.35	50	<i>H. impetiginosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
	75	<i>H. impetiginosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
	100	<i>H. impetiginosus</i>	0.15 ^{de}	0.71 ^{efg}	1.01 ^{de}	0.18 ^{def}
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
7.38	50	<i>H. impetiginosus</i>	0.12 ^{de}	0.23 ^{fg}	0.46 ^e	0.12 ^{ef}
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
	75	<i>H. impetiginosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
	100	<i>H. impetiginosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f
		<i>H. spongiosus</i>	0.00 ^e	0.00 ^g	0.00 ^e	0.00 ^f

The letters (a, b, c, d, e, f, g) represent the significance of the results, after Tukey's tests at 5% significance.

As the salinity of the irrigation water increased, there were reductions in the parameters analysed for both *H. impetiginosus* and *H. spongiosus* (Figure 3). For plant height (PH), there was a decrease of 67%, 95% and 97% for salinity levels SL2, SL3 and SL4, respectively, when compared to the control. When subjected to the highest salinity level (SL4), reductions

of 93% and 98% were seen for the variables height (PH), collar diameter (CD), number of leaves (NL), dry leaf biomass (DLB), dry stem biomass (DSB), dry root biomass (DRB), total dry biomass (TDB) and collar diameter/height ratio (CD/PH). For total plant dry biomass, it was observed that with each increase of 0.01 dS m^{-1} , there was a reduction of up to 4% in the accumulation of dry matter. These effects were significant for water use efficiency (WUE), which fell by up to 95% in SL4 compared to the control treatment, demonstrating that the species is sensitive to exposure to salts in the soil.

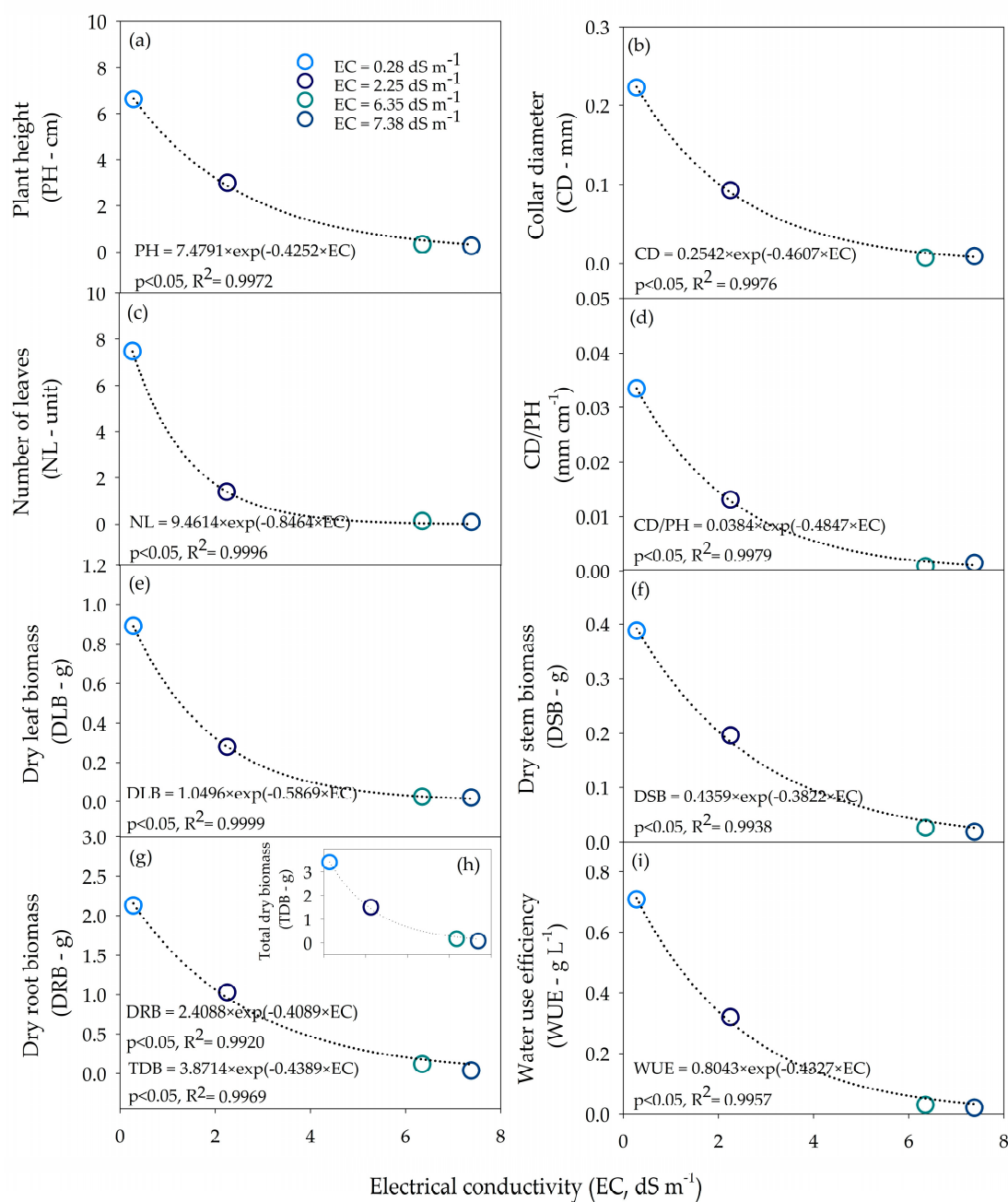


Figure 3. Responses of the variables plant height [PH—cm] (a), collar diameter [CD—mm] (b), number of leaves [NL—units] (c), collar diameter to plant height ratio [CD/PH— mm cm^{-1}] (d), dry leaf biomass [DLB—g] (e), dry stem biomass [DSB—g] (f), dry root biomass [DRB—g] (g), total dry biomass [TDB—g] (h), and water use efficiency [WUE— g L^{-1}] (i), for the species *H. impetiginosus* and *H. spongiosus* submitted to different levels of salinity represented by the following electrical conductivities (EC) of the irrigation water: 0.27, 2.52, 6.35 and 7.38 dS m^{-1} , Serra Talhada-PE, Brazil.

Unlike salinity, the water depths applied did not have a significant influence on the variables analysed in both species, *H. impetiginosus* and *H. spongiosus*. For plant height (Figure 4a), the 50% water depth showed no statistical difference compared to the 100% and 75% ETo levels, with standard errors of 54%, 65% and 52%, respectively. However, when looking at the variables number of leaves (Figure 4b), root biomass (Figure 4c), total biomass (Figure 4d) and collar diameter (Figure 4e), the depth of 100% ETo showed the best results, while there was no significant difference between the other applied depths.

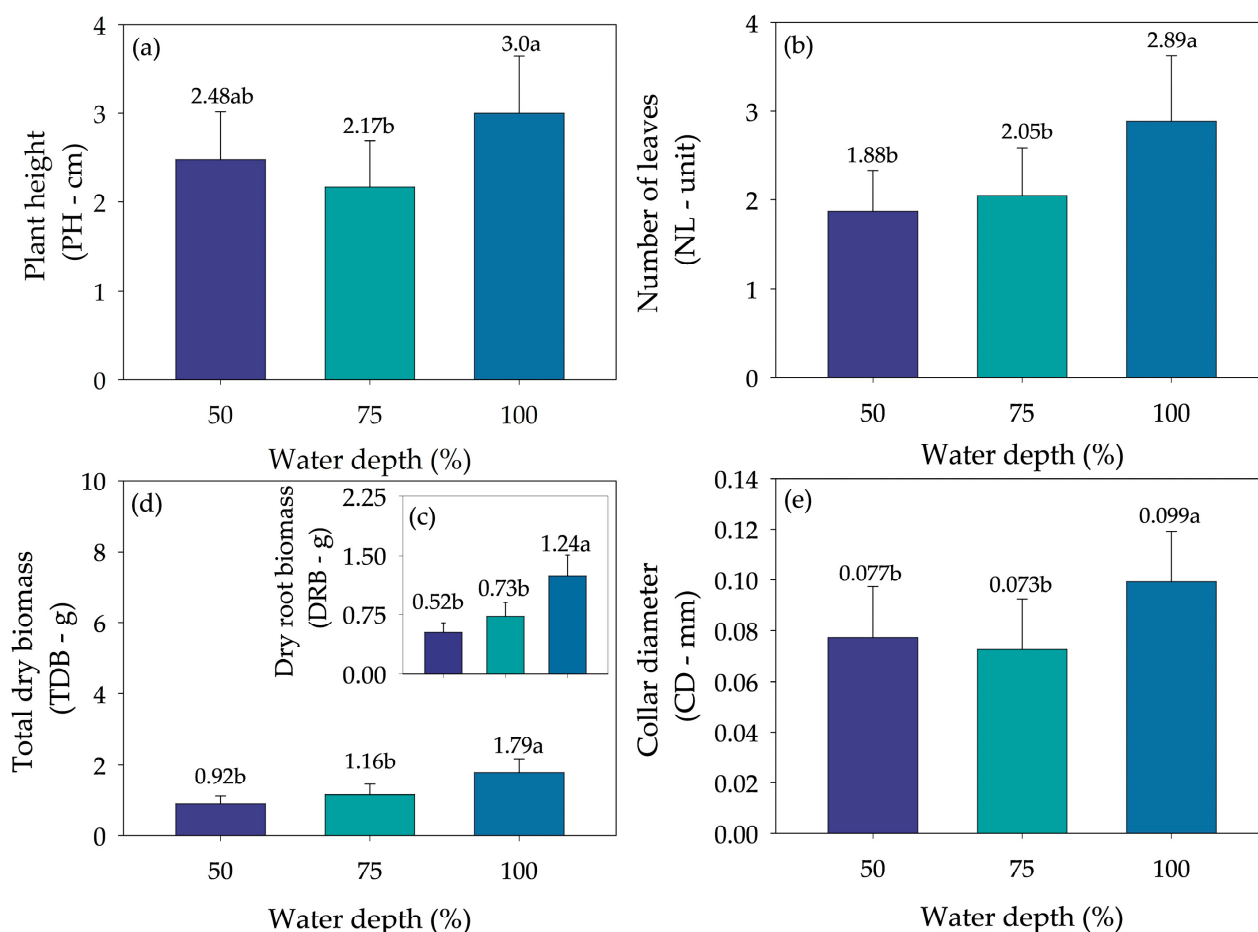


Figure 4. Responses of the variables plant height [PH—cm] (a), number of leaves [NL—unit] (b), dry root biomass [DRB—g] (c), total dry biomass [TDB—g] (d) and collar diameter [CD—mm] (e), for the species *H. impetiginosus* and *H. spongiosus* submitted to different irrigation depths (50%, 75% and 100% ETo), Serra Talhada-PE, Brazil. Error bars represent the standard deviation of the mean, above the bars are the mean and the letters represent the significance levels of Tukey's test.

For the species factor, *H. impetiginosus* stood out as the most tolerant, showing a significant increase in the growth variables analysed. Compared to *H. spongiosus*, *H. impetiginosus* showed an increase of 185% in height, 206% in total dry biomass and 205% in water use efficiency, with standard errors of 48%, 21% and 5%, respectively (Figure 5). This indicates that the species responds more efficiently to stress conditions, demonstrating a greater capacity to adapt than *H. spongiosus*. The interaction between salinity levels and water depths for both species (Table 3) revealed significant reductions in all analysed parameters as salinity increased and water availability decreased. Under the 100% ETo water depth, plant height showed reductions of 58%, 87% and 100% at salinity levels SL2, SL3 and SL4, respectively, when compared to SL1.

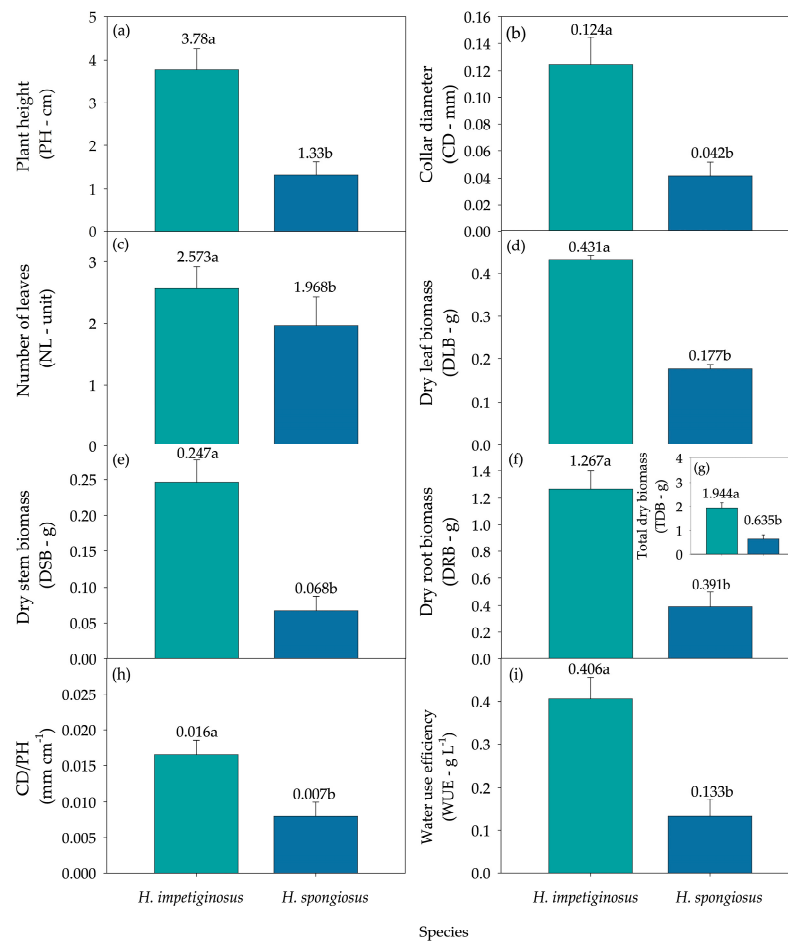


Figure 5. Response of the species *H. impetiginosus* and *H. spongiosus*. Plant height [PH—cm] (a), collar diameter [CD—mm] (b), number of leaves [NL—units] (c), dry leaf biomass [DLB—g] (d), dry stem biomass [DSB—g] (e), dry root biomass [DRB—g] (f), total dry biomass [TDB—g] (g), collar diameter to plant height ratio [CD/PH—mm cm^{−1}] (h) and water use efficiency [WUE—g L^{−1}] (i). Error bars represent the standard deviation of the mean, above the bars are the mean and the letters represent the significance levels of Tukey's test.

Table 3. Effects of water depth (50% ETo, 75% ETo and 100% ETo) and salinity levels (SL1 = 0.278 dS m^{−1}, SL2 = 2.252 dS m^{−1}, SL3 = 6.35 dS m^{−1} and SL4 = 7.38 dS m^{−1}) on plant height (PH—cm), collar diameter (CD—mm), number of leaves (NL—unit), dry leaf biomass (DLB—g), dry root biomass (DRB—g), total dry biomass (TDB—g) and water use efficiency (WUE—g L^{−1}).

Water depth (%)	Plant height (cm)			
	0.27 dS m ^{−1}	2.25 dS m ^{−1}	6.35 dS m ^{−1}	7.38 dS m ^{−1}
50	5.72 ^b	3.41 ^c	0.00 ^e	0.78 ^{de}
75	6.37 ^{ab}	2.31 ^{cd}	0.00 ^e	0.00 ^e
100	7.75 ^a	3.25 ^c	1.00 ^{de}	0.00 ^e
Water depth (%)	Collar diameter (mm)			
	0.27 dS m ^{−1}	2.25 dS m ^{−1}	6.35 dS m ^{−1}	7.38 dS m ^{−1}
50	0.18 ^b	0.10 ^c	0.00 ^e	0.03 ^{de}
75	0.22 ^b	0.07 ^{cd}	0.00 ^e	0.00 ^e
100	0.27 ^a	0.10 ^c	0.02 ^{de}	0.00 ^e

Table 3. Cont.

Water depth (%)	0.27 dS m ⁻¹	Number of leaves (unit)		
		0.27 dS m ⁻¹	2.25 dS m ⁻¹	6.35 dS m ⁻¹
50	5.62 ^b	1.62 ^c	0.00 ^c	0.25 ^c
75	7.06 ^b	1.12 ^c	0.00 ^c	0.00 ^c
100	9.75 ^a	1.4 ^c	0.37 ^c	0.00 ^c
Water depth (%)	0.27 dS m ⁻¹	Dry leaf biomass (g)		
		0.27 dS m ⁻¹	2.25 dS m ⁻¹	6.35 dS m ⁻¹
50	0.56 ^b	0.32 ^{bc}	0.00 ^c	0.06 ^c
75	1.01 ^a	0.20 ^{bc}	0.00 ^c	0.00 ^c
100	1.10 ^a	0.32 ^{bc}	0.07 ^c	0.00 ^c
Water depth (%)	0.27 dS m ⁻¹	Dry root biomass (g)		
		0.27 dS m ⁻¹	2.25 dS m ⁻¹	6.35 dS m ⁻¹
50	1.21 ^{cd}	0.76 ^{cd}	0.00 ^d	0.12 ^d
75	2.09 ^b	0.81 ^{cd}	0.00 ^d	0.00 ^d
100	3.08 ^a	1.52 ^{bc}	0.36 ^d	0.00 ^d
Water depth (%)	0.27 dS m ⁻¹	Total dry biomass (g)		
		0.27 dS m ⁻¹	2.25 dS m ⁻¹	6.35 dS m ⁻¹
50	2.13 ^c	1.31 ^{cd}	0.00 ^f	0.23 ^{ef}
75	3.48 ^b	1.18 ^{cde}	0.00 ^f	0.00 ^f
100	4.62 ^a	2.02 ^c	0.51 ^{def}	0.00 ^f
Water depth (%)	0.27 dS m ⁻¹	Water use efficiency (g L ⁻¹)		
		0.27 dS m ⁻¹	2.25 dS m ⁻¹	6.35 dS m ⁻¹
50	0.57 ^{cd}	0.35 ^d	0.00 ^f	0.06 ^{ef}
75	0.74 ^{ab}	0.25 ^{de}	0.00 ^f	0.00 ^f
100	0.81 ^a	0.35 ^{cd}	0.09 ^{ef}	0.00 ^f

The letters (a, b, c, d, e, f) represent the significance of the results, after Tukey's tests at 5% significance.

For the effects of the interaction between species and salinity levels (Table 4), it was found that for both species the control treatment was more representative than the other salinity levels; however, when analysing the species, it can be seen that *H. impetiginosus* showed higher results than *H. spongiosus* in the control and SL2 treatments, highlighting its tolerance to the treatments applied. When the effects of the water depths and species association were analysed (Table 5), it could be seen that for the parameters plant height and collar diameter, *H. impetiginosus* obtained the best results in all the irrigation depths applied, showing increases of approximately 33% and 65%, respectively, compared to *H. spongiosus* at the lowest salinity level.

Table 4. Effects of the interaction between species and salinity levels (SL1 = 0.278 dS m⁻¹, SL2 = 2.252 dS m⁻¹, SL3 = 6.35 dS m⁻¹ and SL4 = 7.38 dS m⁻¹) on plant height (PH—cm), collar diameter (CD—mm), number of leaves (NL—unit), dry leaf biomass (DLB—g), dry stem biomass (DSB—g), dry root biomass (DRB—g), total dry biomass (TDB—g), diameter/height ratio (CD/PH—cm mm⁻¹) and water use efficiency (WUE—g L⁻¹).

Salinity levels	Plant height (cm)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	7.94 ^a	5.98 ^b
2.25	5.29 ^b	0.00 ^c
6.35	0.67 ^c	0.00 ^c
7.38	0.52 ^c	0.00 ^c

Table 4. Cont.

Salinity levels	Collar diameter (mm)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	0.28 ^a	0.17 ^b
2.25	0.18 ^b	0.00 ^c
6.35	0.01 ^c	0.00 ^c
7.38	0.02 ^c	0.00 ^c
Salinity levels	Number of leaves (unit)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	7.08 ^a	7.87 ^a
2.25	2.79 ^b	0.00 ^c
6.35	0.25 ^c	0.00 ^c
7.38	0.17 ^c	0.00 ^c
Salinity levels	Dry leaf biomass (g)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	1.08 ^a	0.71 ^b
2.25	0.56 ^b	0.00 ^c
6.35	0.05 ^c	0.00 ^c
7.38	0.04 ^c	0.00 ^c
Salinity levels	Dry stem biomass (g)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	0.50 ^a	0.27 ^c
2.25	0.39 ^b	0.00 ^c
6.35	0.05 ^c	0.00 ^c
7.38	0.04 ^c	0.00 ^c
Salinity levels	Dry root biomass (g)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	2.69 ^a	1.56 ^b
2.25	2.06 ^b	0.00 ^c
6.35	0.24 ^c	0.00 ^c
7.38	0.08 ^c	0.00 ^c
Salinity levels	Total dry biomass (g)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	4.27 ^a	2.54 ^b
2.25	3.01 ^b	0.00 ^c
6.35	0.34 ^c	0.00 ^c
7.38	0.15 ^c	0.00 ^c
Salinity levels	CD/PH (mm cm ⁻¹)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	0.03 ^a	0.03 ^{ab}
2.25	0.03 ^{ab}	0.00 ^c
6.35	0.00 ^c	0.00 ^c
7.38	0.00 ^c	0.00 ^c
Salinity levels	Water use efficiency (g L ⁻¹)	
(dS m ⁻¹)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
0.27	0.88 ^a	0.53 ^b
2.25	0.64 ^b	0.00 ^c
6.35	0.06 ^c	0.00 ^c
7.38	0.04 ^c	0.00 ^c

The letters (a, b, c) represent the significance of the results, after Tukey's tests at 5% significance.

Table 5. Effects of the interaction between species (*H. impetiginosus* and *H. spongiosus*) and water depths (50%, 75% and 100% ETo) on plant height (PH—cm), collar diameter (CD—mm), dry leaf biomass (DLB—g), dry root biomass (DRB—g) and water use efficiency (WUE—g L^{−1}).

Water depth	Plant height (cm)	
(%)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
50	3.91 ^{ab}	1.05 ^c
75	3.03 ^b	1.31 ^c
100	4.39 ^a	1.61 ^c
Water depth	Collar diameter (mm)	
(%)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
50	0.12 ^{ab}	0.03 ^c
75	0.10 ^b	0.04 ^c
100	0.15 ^a	0.05 ^c
Water depth	Dry leaf biomass (g)	
(%)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
50	0.37 ^{ab}	0.32 ^b
75	0.10 ^c	0.29 ^{bc}
100	0.60 ^a	0.14 ^{bc}
Water depth	Dry root biomass (g)	
(%)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
50	0.86 ^b	0.18 ^c
75	0.94 ^b	0.51 ^{bc}
100	2.00 ^a	0.47 ^{bc}
Water depth	Water use efficiency (g L ^{−1})	
(%)	<i>H. impetiginosus</i>	<i>H. spongiosus</i>
50	0.40 ^{ab}	0.09 ^d
75	0.31 ^{bc}	0.18 ^{cd}
100	0.51 ^a	0.12 ^d

The letters (a, b, c, d) represent the significance of the results, after Tukey's tests at 5% significance.

During the course of the experiment, there was an accumulation of 2267.74 ADD. When the responses of the plant height (Figure 6), collar diameter (Figure 7) and number of leaves (Figure 8) variables were analysed as a function of accumulated degree days over the course of the experiment, it was noted that over the course of the days, the plants subjected to salinity levels SL2, SL3 and SL4 at all water depths showed a regression in the parameters evaluated. However, for the control treatment, the irrigation depth of 100% ETo showed linear growth over time. In addition, there was different growth for the species analysed, with more pronounced sensitivity to SL exposure than to RH variation.

Our results indicate that *H. impetiginosus* showed greater efficiency in leaf growth under the tested abiotic conditions (Table 6). Considering the leaf emergence rate (LER), this species performed approximately 54.5% better than *H. spongiosus*. Over the total thermal accumulation of 2267.74 °C day, *H. impetiginosus* produced an average of 11.71 leaves per plant, while *H. spongiosus* produced only 7.57 leaves. These results suggest that *H. impetiginosus* exhibits a more efficient leaf growth strategy, possibly associated with greater tolerance to the imposed environmental conditions.

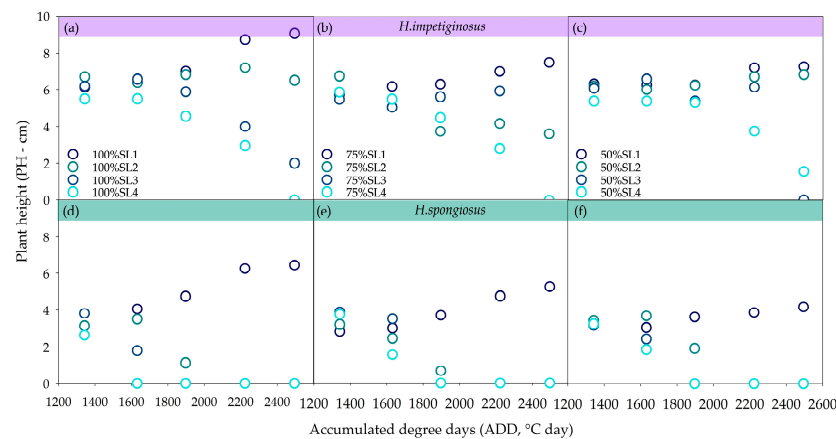


Figure 6. Response of the plant height (PH—cm) variable as a function of the accumulation of degree days of the species *H. impetiginosus* and *H. spongiosus*, subjected to water depths (WDs): 50%, 75% and 100% ETo at salinity levels (SL) of 0.28, 2.52, 6.35 and 7.38 dS m⁻¹, in Serra Talhada-PE, Brazil. Panels (a–c) represent the applications of 100, 75 and 50% ETo slides on *H. impetiginosus*, and panels (d–f) for *H. spongiosus*.

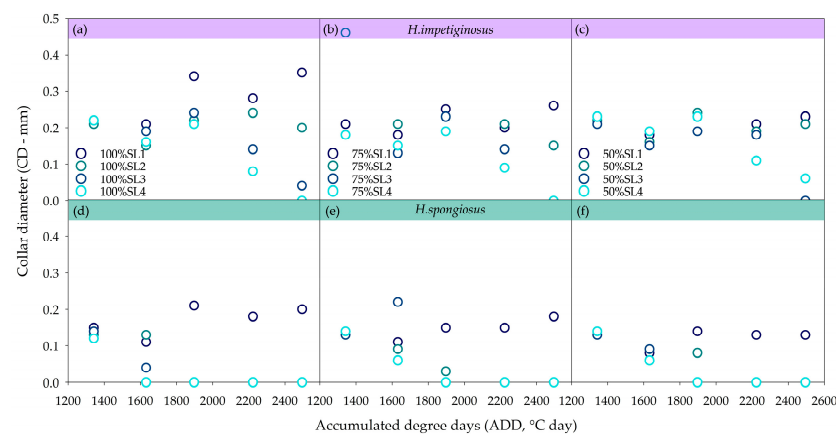


Figure 7. Response of the collar diameter (CD—mm) variable as a function of the accumulation of degree days of the species *H. impetiginosus* and *H. spongiosus*, submitted to water depths (WDs): 50%, 75% and 100% ETo at salinity levels (SL) of 0.28, 2.52, 6.35 and 7.38 dS m⁻¹, in Serra Talhada-PE, Brazil. Panels (a–c) represent the applications of 100, 75 and 50% ETo slides on *H. impetiginosus*, and panels (d–f) for *H. spongiosus*.

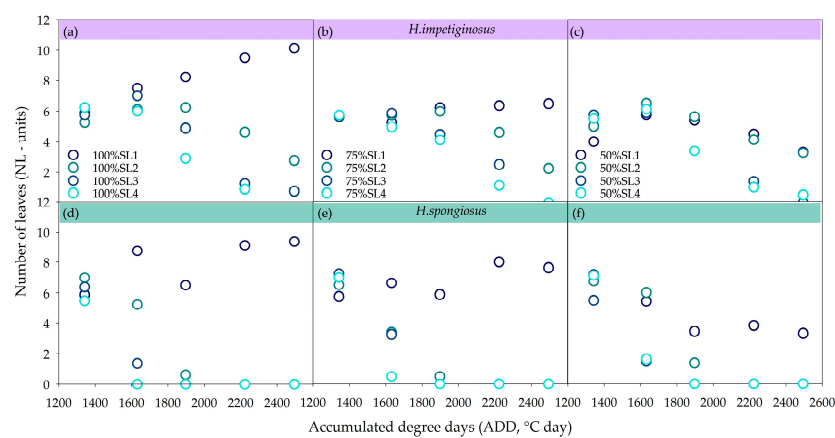


Figure 8. Response of the number of leaves (NL—units) as a function of the accumulation of degree days of the species *H. impetiginosus* and *H. spongiosus*, submitted to water depths (WDs): 50%, 75% and 100% ETo at salinity levels (SL) of 0.28, 2.52, 6.35 and 7.38 dS m⁻¹, in Serra Talhada-PE, Brazil. Panels (a–c) represent the applications of 100, 75 and 50% ETo slides on *H. impetiginosus*, and panels (d–f) for *H. spongiosus*.

Table 6. Leaf emergence rate (LER) and phyllochron of *H. impetiginosus* and *H. spongiosus* subjected to irrigation depths of 50%, 75% and 100% of ETo under different salinity levels in Serra Talhada-PE, Brazil. Dates are expressed in the following format: mm/dd/yyyy.

Date	Specie	Mean Number of Leaves (Unit)	LER (Leaf ADD ^{−1})	Phyllochron (ADD Leaf ^{−1})
09/20/2023	<i>H. impetiginosus</i>	5.88	0.0052	192.55
	<i>H. spongiosus</i>	5.00	0.0044	226.24
10/05/2023	<i>H. impetiginosus</i>	6.00	0.0095	234.07
	<i>H. spongiosus</i>	5.00	0.0035	280.88
10/20/2023	<i>H. impetiginosus</i>	6.50	0.0040	256.90
	<i>H. spongiosus</i>	5.00	0.0032	303.61
11/05/2023	<i>H. impetiginosus</i>	7.00	0.0035	285.11
	<i>H. spongiosus</i>	6.00	0.0030	332.63
11/20/2023	<i>H. impetiginosus</i>	8.20	0.0036	276.55
	<i>H. spongiosus</i>	6.00	0.0026	377.95

4. Discussion

As the results show, the increase in salinity influenced all the parameters assessed in the study. This can be explained by the toxicity of the salts in the tissues and the accumulation of ions inside the plant and in the soil, which prevent the roots from absorbing water and developing properly. The work carried out by Sousa Neto et al. [36] showed that the increase in osmotic pressure caused by excess salts reduced water absorption by the roots, affecting the growth of the species *Mimosa caesalpiniiifolia* and *Mimosa tenuiflora*, consequently reducing the accumulation of total dry mass. It should be remembered that excess salts cause water restriction in plants. Under water deficit, photosynthetic products are reduced due to stomatal closure and the reduction of CO₂ inside the cells, resulting in lower plant growth. Moreover, excess salts can alter the biochemical properties of plants through oxidative stress, which promotes chlorophyll degradation and damages photosynthetic proteins [37]. However, the phenological stage and the intensity of the stress on the plant are factors that influence its response, as is the case with dry biomass [38].

Total dry biomass decreased progressively as electrical conductivity increased. This reduction in plant growth and dry matter production under saline stress is mainly caused by water restriction due to osmotic imbalance, leading to stomatal closure and the toxicity of salt accumulation within the plant [39]. As a result, as salinity increased, water use efficiency decreased, indicating that the species were unable to carry out their metabolic functions efficiently [40]. Similar results were obtained by Azeem et al. [41] when studying the species *Moringa oleifera*. The authors reported that, under salt stress, a large portion of energy is diverted to defence mechanisms, which reduces plant growth and consequently limits biomass accumulation. Root biomass, on the other hand, is affected by the decrease in root development to limit the entry of salts during the absorption of water from the soil [42].

Among the defence mechanisms adopted by plants under salt stress, the ability to perceive and transduce osmotic and ionic signals into the interior of cells stands out. Increased salinity stimulates the formation of reactive oxygen species (ROS), which, in excess, can cause DNA damage [43]. However, during the absorption process by the roots, plants are able to exclude a significant portion of salts, preventing the accumulation of ions within the cells [44]. In addition, many plants accumulate compounds such as proline and

soluble sugars, which act as osmoprotectants, helping to maintain cellular osmotic balance and mitigate the toxic effects caused by ion accumulation [45].

Interestingly, among the studied species, *H. impetiginosus* exhibited a higher growth rate compared to *H. spongiosus*. Its growth is explained by its adaptations to environmental stresses, with some adaptive strategies such as leaf senescence, reduced leaf area, decreased dry biomass production and modifications to the root system [18,46]. On the other hand, *H. spongiosus*, as seen by Ferreira et al. [47], is classified as a species that is not very tolerant to saline and water stress, which would explain the losses obtained in all treatments with high salt concentrations, resulting only in the survival of the individuals present in the control treatment. Under more stressful abiotic conditions, the plants died. Although *H. impetiginosus* demonstrated better performance, the increase in salinity led to a regression in growth, a common behaviour in deciduous species of the Caatinga, which are characterised by high wood density, lower water potential and moderate water use efficiency, providing some tolerance to water stress [48].

Caatinga species have limited growth to ensure the functioning of their physiological functions [49]. These authors studied the species *Myracrodruon urundeuva*, *Mimosa caesalpinhiifolia* and *H. impetiginosus*, and their results highlighted that when subjected to saline stress, the dry biomass of the leaves was affected. One explanation for this decrease is the decrease in the production of photosynthesis, resulting in a decrease in the growth of the species. Another determining factor for plant growth affected by salinity is cell elongation. High salt concentrations decrease the activity of alpha- and beta-galactosidases, enzymes that mediate this process, resulting in a decrease in plant development [50].

When observing the responses of the height, collar diameter and number of leaves of the species studied in relation to the accumulated degree days, it can be seen that only under potential conditions was the growth of these variables maximised, and as the level of salinity increased, the reductions in growth were more pronounced. Under natural and controlled conditions, plants can alter their morphology as a mechanism to remain in the environment [9,49]. In this case, changes in the amount of energy needed to produce a leaf were also observed, so that this tended to increase the lower the water depth and under high saline exposure. Araújo et al. [51], when studying forest species, observed phyllochron values for the species *H. heptaphyllus* equal to 122.5 ADD leaf⁻¹. According to the authors, the greater the accumulation of energy needed to produce a leaf, the less the species develops. This behaviour indicates that the species is more sensitive to increased salinity than to water deficit, which represents an adaptive mechanism for maintaining its vital conditions.

5. Conclusions

This research evaluated the growth responses of the species *H. impetiginosus* and *H. spongiosus* under combined water and salinity stresses as an alternative recommendation in areas with desertification problems. It was observed that *H. impetiginosus* showed greater tolerance to the conditions tested compared to *H. spongiosus*, demonstrating potential for ecological restoration programmes in Caatinga environments. Salt stress had a significant negative impact on the growth and dry biomass accumulation of both species. In addition, water deficit affected the height, collar diameter, number of leaves, root biomass and total biomass of the plants. Initial water replenishment based on 100% ETo proved to be the most effective for both species. Although it showed lower tolerance, the use of *H. spongiosus* should not be ruled out, especially in environments with lower stress levels or when management strategies are adopted to mitigate water and salt stress. The ecological importance of both species supports their inclusion in initiatives aimed at preserving the Caatinga biome.

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