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Response of Morphological Characters and Photosynthetic Characteristics of *Haloxylon ammodendron* to Water and Salt Stress

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Abstract: In arid desert areas, *Haloxylon ammodendron* plays an important role in maintaining the ecological balance of desert oases. However, there are few studies on the physiological characteristics of *Haloxylon ammodendron* under an environmental gradient. Here, we studied the changes in the morphological and photosynthetic characteristics and their correlations in *Haloxylon ammodendron* in the four habitats of the Ebinur Lake wetland. Our results show that in high-water and high-salt habitats, photosynthesis is affected by "stomata restriction," while in other habitats, photosynthesis is mainly affected by "non-stomata restriction." In addition, when the soil conditions were good, *Haloxylon ammodendron* chose leaf construction featuring high specific leaf area, while when the soil conditions were worse, it chose an opposite leaf construction model to ensure the optimal allocation of carbon assimilation products in heterogeneous habitats. This study will deepen our understanding of the trade-off strategy between the accumulation and distribution of plant photosynthate in special habitats in arid areas. The results are of theoretical value for analysis of the ecological adaptation mechanisms of plants in arid desert areas.

Keywords: *Haloxylon ammodendron*; morphological traits; photosynthetic characteristics; soil water-salt stress

Citation: Hu, D.; Lv, G.; Qie, Y.; Wang, H.; Yang, F.; Jiang, L. Response of Morphological Characters and Photosynthetic Characteristics of *Haloxylon ammodendron* to Water and Salt Stress. *Sustainability* **2021**, *13*, 388. https://doi.org/10.3390/su13010388

Received: 13 November 2020
Accepted: 31 December 2020
Published: 4 January 2021

1. Introduction

In arid and semi-arid areas, water and salt are the main environmental factors limiting plant growth. The morphological structure and photosynthetic characteristics of plants will change according to the soil water and salt contents. Once the soil water content decreases, the plant will develop a more simple, low-lying structure. At the same time, drought stress causes leaf stomata to close and mesophyll cells to become damaged; photosynthetic enzyme activity is decreased, the chloroplast structure may be destroyed, chlorophyll content may be decreased, and the photosynthetic rate of plants will be decreased [1,2]. A large amount of salt ions in the soil will stress the growth of plants and increase the concentration of salt ions in plant cells above the tolerance range of many enzymes, resulting in the denaturation and inactivation of enzymes [3,4]. In addition, salt stress also affects the components, permeability, transport, and ion flow of the plant plasma membrane, leading to damage to the normal functioning of the cell membrane. This in turn affects the metabolism and physiological functions of plant cells to varying degrees, thus affecting the physiological characteristics of plants [5]. Under altered soil water and salt conditions, plants need to balance the distribution of leaf carbon assimilation products by adjustments in leaf thickness, specific leaf area, and other leaf characteristics, and leaf photosynthesis can be adjusted by changes in electron transfer rate and light energy distribution. The effective utilization of light energy absorbed by plants reflects the synergistic adaptation mechanism between leaf characteristics and leaf photosynthetic physiological characteristics [6].

Haloxylon ammodendron is a remnant of the ancient Mediterranean flora and is mainly distributed in desert areas with low rainfall (30–200 mm) in Africa and Asia. Owing to its highly developed root system, the plant has many adaptive characteristics such as drought resistance, high-temperature resistance, salt and alkali resistance, wind erosion resistance, and cold resistance. *Haloxylon ammodendron* has become the largest tree species for dune fixation afforestation in the arid desert of northwest China. The species thus plays an important role in maintaining the ecological balance between desert and oasis [7]. To adapt to the extremely scarce soil moisture and intense high-temperature transpiration environment, in *Haloxylon ammodendron*, photosynthesis is conducted by green twigs (assimilation twigs) that degenerate into scaly and fleshy leaves. Among meteorological elements, temperature and precipitation are important climatic factors affecting soil moisture. Climate change can lead to changes in soil moisture, and changes in soil moisture can also have a certain impact on the climate. Since the end of 1980s, the climate in Xinjiang Uygur autonomous region has been warming and humidifying as a result of global climate change [8]. In the past 20 years since the beginning of the 21st century, there have been two trends in Xinjiang Uygur autonomous region's climate: one is that the total precipitation in Xinjiang Uygur autonomous region continues to increase; the other is that extreme precipitation events have fluctuated and increased [9], significantly affecting the vegetation in the desert areas [10]. Therefore, the study of morphological and photosynthetic characteristics of *Haloxylon ammodendron* under water and salt gradient will provide scientific basis for the response of *Haloxylon ammodendron* to global change.

In recent years, ecologists have studied the physiological characteristics of *Haloxylon ammodendron* under salt stress [11–13] or the effects of dust in mining areas on photosynthesis [14,15], and most of these studies have been realized through controlled experiments rather than through in situ experiments. In contrast, there are few studies on the physiological characteristics of *Haloxylon ammodendron* under water stress or the double stress of water and salt. In the desert area of Aibihu Wetland National Nature Reserve, across from the Aqikesu River, there is a natural water-salt gradient that provides optimal environmental conditions for in situ experiments. Therefore, taking *Haloxylon ammodendron* in the Ebinur lake basin as the research object, analyzing the morphological adjustments and changes in photosynthetic characteristics under different water and salt gradients addresses the following questions: (1) How do the morphological characters and gas exchange parameters of *Haloxylon ammodendron* change under different water and salt gradients? (2) What are the growth indexes that mainly affect the photosynthetic characteristics of *Haloxylon ammodendron*? The study aims to enrich our knowledge and understanding of the survival strategies of plants, and have theoretical value concerning the mechanism of desert plants adapting to stresses in arid areas.

2. Materials and Methods

2.1. Study site and Experimental Design

The study was performed in the Aibihu Wetland National Nature Reserve in Jinghe County, Xinjiang Uygur autonomous region (82°33′–83°53′ E, 44°31′–45°09′ N). This area is located in the northwest inland region of China and is characterized by extreme drought and little rain, abundant sunshine, and large temperature differences between day and night typical of a temperate continental arid climate [16]. The annual average temperature is 7.8 °C, the extreme minimum temperature is −36.4 °C, and the extreme maximum temperature is 41.3 °C [17]. Soil types are mainly grey-brown desert soil and aeolian sandy and salinized soil. There are abundant species of desert xerophytes, including *Haloxylon ammodendron*, *Populus euphratica*, *Tamarix chinensis*, *Calligonum mongolicum*, *Reaumuria songonica*, *Halostachys caspica*, *Alhagi sparsifolia*, and *Phragmites australis*.

In the desert area of Aibihu Wetland National Nature Reserve near the Aqikesu River, there is a natural water and salt gradient, and the soil moisture and salinity content decrease with distance from the river. From July to August 2017, a 3630 m × 30 m transect was set up to the north of the Aqikesu River (Figure 1). Within the transect, a 30 m × 30 m quadrat was selected every 90 m, a total of 31 quadrats. In each quadrat, two mature and healthy *Haloxylon ammodendron* plants were selected as test plants; if there was no plant in a certain quadrat or the growth was not well, the nearest one was selected laterally outside the quadrat. A total of 62 trees were selected.

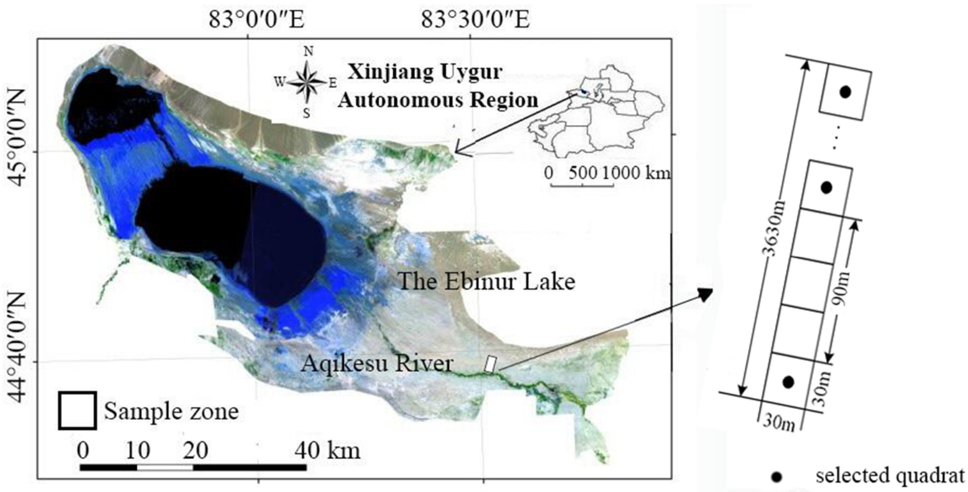

Figure 1. Location of the study area and the investigated plots.

2.2. Collection and Determination of Soil Samples

A soil profile with a depth of 50 cm was dug from the north and south sides of each tested plant using a spade, and the soil was divided into three sampling layers of 0–10 cm, 10–30 cm, and 30–50 cm. First, each layer of soil was placed into an aluminum box for the determination of soil water content; second, another soil sample was placed in a self-sealing bag and brought back to the laboratory for natural air drying. The measured soil indexes included water content (WC), salt content (SC), organic matter (SOM), total phosphorus (TP), and total nitrogen, (TN). The soil index determination methods are shown in Table 1.

Table 1. Soil index and determination method.

Soil Factors	Method
Soil water content	Drying method
Soil pH	Electrode potential method
Soil salt content	Residue from an oven drying method
Soil organic matter	Potassium dichromate volumetric method-external heating method
Soil total phosphorus	Molybdenum-antimony spectrophotometry method
Soil total nitrogen	Kjeldahl nitrogen determination method

2.3. Plant Growth Determination

The base diameter (BD), tree height (H), east-west length, and north-south length of the tested plants were measured using steel tapes. At the same time, complete and healthy assimilated branches were collected, labeled, bagged, and brought back to the laboratory to measure the leaf area (LA). The leaf thickness (LT) and length of assimilated branches were measured with Vernier calipers. In addition, the fresh weight of leaves was measured with an electronic analytical balance, and then the assimilated branches were dried in an oven at 80 °C to constant weight. The leaf dry weight was measured, and the specific leaf area (SLA) was calculated. The calculation formula was as follows:

$$\text{Specific leaf area} = \text{leaf area}/\text{leaf dry weight}, \quad (1)$$

$$\text{Leaf dry matter content} = \text{leaf dry weight}/\text{leaf wet weight} \times 100\%. \quad (2)$$

2.4. Photosynthetic Measurement

In sunny and windless weather, the photosynthetic parameters of *Haloxylon ammodendron* plants were measured by an LI-6400XT portable photosynthesis measuring system (Li-Cor, Lincoln, NE, USA). The light intensity and CO_2 concentration were controlled using a $2 \times 3 cm^2$ red and blue light source (6400-02B) leaf chamber and CO_2 injection system. The CO_2 concentration was set to 400 μmol·mol^{-1}, and leaf room photon flux density ($PPFD_i$) employed a 15 point gradient of 2400, 2200, 2000, 1800, 1500, 1200, 800, 600, 400, 200, 150, 100, 50, 20, 1, and 0 μmol·mol^{-1}. The velocity was 500 μmol·s^{-1}, and leaf room temperature was controlled to 30 °C. The net photosynthetic rate (P_n, μmol·m^{-2}·s^{-1}), stomatal conductance (G_s, mol·m^{-2}·s^{-1}), transpiration rate (T_r, mmol·m^{-2}·s^{-1}), intercellular CO_2 concentration (C_i, μmol·mol^{-1}), and vapor pressure deficit (VPDL, kPa) of plant leaves under different light intensities were measured. Water use efficiency (WUE) was defined as the ratio of net photosynthetic rate to transpiration rate.

The relationship between photosynthetic rate and light intensity can be fitted by a rectangular hyperbolic correction model [18]:

$$P_n = \alpha \frac{1 - \beta \cdot PAR}{1 + \gamma \cdot PAR} PAR - R_d \quad (3)$$

In this formula, P_n is the net photosynthetic rate (μ mol m^{-2} s^{-1}); PAR is the photosynthetic effective radiation (μmol·m^{-2}·s^{-1}); α is the slope of photosynthesis when PAR = 0, i.e., the initial quantum efficiency (mol mol^{-1}); β is the light suppression coefficient; γ is the light saturation coefficient; and Rd is the dark respiration rate (μ mol m^{-2} s^{-1}).

2.5. Statistical Analysis

Haloxylon ammodendron habitats were divided into four gradients, high water and salt content, medium water and high salt content, medium water and salt content, and low water and salt content, based on the K-means method of the soil water and salt content (Table 2). One-way ANOVA was used to test the significance of differences in environmental factors, morphological characters and photosynthetic physiology of *Haloxylon ammodendron* from four habitats. LSD (Least—Significant Difference) tests (under homogeneity of variance) and the T2 (Tamhane T2) method of Tamhane (for inhomogeneous variance) were used for multiple comparisons. The above analysis was completed in SPSS (IBM Corporation Armonk, New York, NY, USA). Redundancy analysis (RDA) were completed using vegan package of R version 4.0.2(R core team, Vienna, Austria). Other charts were completed using Visio 2016 (Microsoft corporation, Redmond, DC, USA) and Origin 2018 (OriginLab corporation, Northampton, WA, USA).

Table 2. Characteristic values of soil environmental factors under different water and salt gradients.

Clustering Result	Sample Number	Soil Environmental Factors, Mean (SE)					
		WC (%)	SC (g/kg)	pH	SOM (g/kg)	TN (g/kg)	TP (g/kg)
I	1–8,10,22	18.160a (2.095)	9.574a (1.996)	8.519a (0.162)	8.933a (3.362)	1.504a (0.431)	0.636a (0.047)
II	9,11,13–15,17, 18,23,25,27,30	10.324b (1.490)	6.615b (1.028)	8.177b (0.128)	2.685b (0.807)	0.547b (0.141)	0.506b (0.046)
III	12,16,20,21,24,26, 28,29,31,32,34,37	8.840b (1.800)	4.580c (0.267)	8.100b (0.116)	1.757c (0.389)	0.390c (0.055)	0.475c (0.034)
IV	19,33,35,36,38–62	3.551c (1.563)	2.551d (0.756)	7.784c (0.138)	1.135d (0.348)	0.223d (0.053)	0.382d (0.027)

Different lowercase letters indicate significant differences between the same soil factors under different water and salt gradients (mean ± SE) ($P < 0.05$); WC: soil water content; SC: soil salt content; SOM: soil organic matter; TP: soil total phosphorus; TN: soil total nitrogen.

3. Results

3.1. Characteristics of Soil Environmental Factors

The measured values of soil water and salt content under the canopy of 62 *Haloxylon ammodendron* were clustered according to the salinization and drought properties of plant habitats in Ebinur Lake Basin (Table 2). *Haloxylon ammodendron* habitats were divided into four gradients: high water and salt content (I), medium water and high salt content (II), medium water and salt content (III), and low water and salt (IV).

Under different water and salt gradients, the soil salt content (SC), total nitrogen (TN), total phosphorus (TP), organic matter (SOM), and pH were significantly different, while the soil water content (WC) was not significantly different in gradients II and III (Table 2). With the increase of the distance from the Aqikesu River, the soil nutrient content showed a decreasing trend, indicating that the environmental stress intensity of *Haloxylon ammodendron* was increasing. Under all gradients, the soil pH value was about 8.0, indicating that the soil was alkaline and that the degree of salinization was serious.

3.2. Morphological Characters

The results of the morphological analysis showed that there were differences among *Haloxylon ammodendron* plant traits under different water and salt gradients (Table 3), and all three traits showed a decreasing trend with the decrease of water and salt content. There was no significant difference in the basal diameter of *Haloxylon ammodendron* between gradient I and gradient II, but there was a significant difference between gradient III and gradient IV. The plant height under gradient I was significantly higher than that of the other three gradients, but there was no significant difference between gradients II and III. In terms of crown area, there were significant differences among the gradients I, II, and III, while the differences between the gradients III and IV were not significant.

Table 3. Variations of plant traits of *Haloxylon ammodendron* under the water and salt gradient.

Water and Salt Gradient	BD (cm^2)	H (m)	CA (m^2)
I	22.730 ± 2.709a	4.100 ± 0.278a	33.860 ± 4.958a
II	18.710 ± 2.701ab	3.270 ± 0.194b	20.870 ± 5.201b
III	12.930 ± 0.973b	2.830 ± 0.160bc	11.010 ± 1.974c
IV	10.210 ± 0.466b	2.520 ± 0.094c	8.730 ± 0.750c

Different lowercase letters indicate significant differences between the same traits under different water and salt gradients (mean ± SE) ($P < 0.05$). BD: base diameter; H: tree height; CA: crown area.

There was no significant difference in thickness or area of assimilated branches of *Haloxylon ammodendron* under the four water and salt gradients, and there was no relatively consistent change rule. The content of assimilated branches increased with the decrease of water and salt content, and there were significant differences between the I and IV gradients, but there were no significant differences among gradients I, II, and III. However, the specific leaf area decreased with the decrease of water and salt content, and there were significant differences between the I gradient and the III and IV gradients, but there were no significant differences between the I gradient and II gradient or between the II gradient and III gradient (Table 4).

Table 4. Variations of assimilating branch traits of *Haloxylon ammodendron* under the water and salt gradient.

Water and Salt Gradient	LT (mm)	LA (cm^2)	LDMC (%)	SLA (cm^2/g)
I	1.049 ± 0.029a	3.186 ± 0.132a	28.107 ± 0.559a	111.113 ± 2.892a
II	1.015 ± 0.048a	3.063 ± 0.371a	28.576 ± 0.547a	100.940 ± 3.606ab
III	1.078 ± 0.046a	3.575 ± 0.414a	29.400 ± 0.770a	92.566 ± 2.857b
IV	1.057 ± 0.030a	3.187 ± 0.188a	36.434 ± 1.377b	76.396 ± 3.488c

Different lowercase letters indicate significant differences between the same traits under different water and salt gradients (mean ± SE) ($P < 0.05$); LT: leaf thickness; LA: leaf area; LDMC: leaf dry matter content; SLA: specific leaf area.

3.3. Photosynthetic Physiology

The results of the gas exchange parameters analysis showed that there were differences among *Haloxylon ammodendron* plant traits under different water and salt gradients (Figure 2). Specifically, C_i increased slightly among the four gradients, and the gradient I was significantly lower than the gradient IV. P_n and WUE showed a relatively consistent change rule; that is, gradient I was significantly larger than the other three gradients and showed an increasing trend among the gradients II, III, and IV. VPDL displayed an opposite trend to P_n and WUE, with a decreasing trend among gradients II, III, and IV, and the gradients I and IV were significantly lower than II and III. There were no significant differences in G_s or T_r under the four gradients, and G_s did not show a relatively consistent change rule under the four gradients. T_r showed an upward trend among gradients I, II, and III, and gradient IV was basically the same as gradient I.

The fitting degree of photosynthesis-light response curves of *Haloxylon ammodendron* was high (Table 5), and the analysis results showed that there was no significant difference in the apparent quantum efficiency (AQY) under four water and salt gradients; the maximum net photosynthetic rate ($P_{n\,max}$) under gradient I was significantly higher than that under the other three gradients. The light compensation point (LCP) and dark respiration rate (R_d) under gradients II and III were significantly higher than those under gradients I and IV. The light saturation point of gradient II was significantly higher than that of gradients III and IV, and the light saturation points of the four gradients were about 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, indicating that the photoinhibition of *Haloxylon ammodendron* will occur when the photosynthetic effective radiation is higher than 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Table 5. Variations of photosynthetic parameters of light response curves of *Haloxylon ammodendron* under the water and salt gradient.

Gradient	$P_{n\,max}$ ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	AQY ($mol \cdot mol^{-1}$)	LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	LSP ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	R_d ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
I	20.919 ± 1.058a	0.039 ± 0.0020a	244.943 ± 37.923a	1981.105 ± 128.396ac	8.480 ± 1.351a
II	15.824 ± 1.046b	0.036 ± 0.002a	473.184 ± 43.066b	2259.406 ± 134.515ab	13.523 ± 1.230b
III	16.430 ± 0.886b	0.038 ± 0.001a	379.480 ± 42.779b	1844.776 ± 61.077c	11.751 ± 1.176b
IV	16.390 ± 0.688b	0.038 ± 0.001a	281.991 ± 23.226a	1920.300 ± 56.869c	8.753 ± 0.616a

Different lowercase letters indicate significant differences between the same photosynthetic parameters under different water and salt gradients (mean ± SE) ($P < 0.05$); $P_{n\,max}$: the maximum net photosynthetic rate; AQY: the apparent quantum efficiency; LCP: the light compensation point; LSP: the light saturation point; R_d: the dark respiration rate.

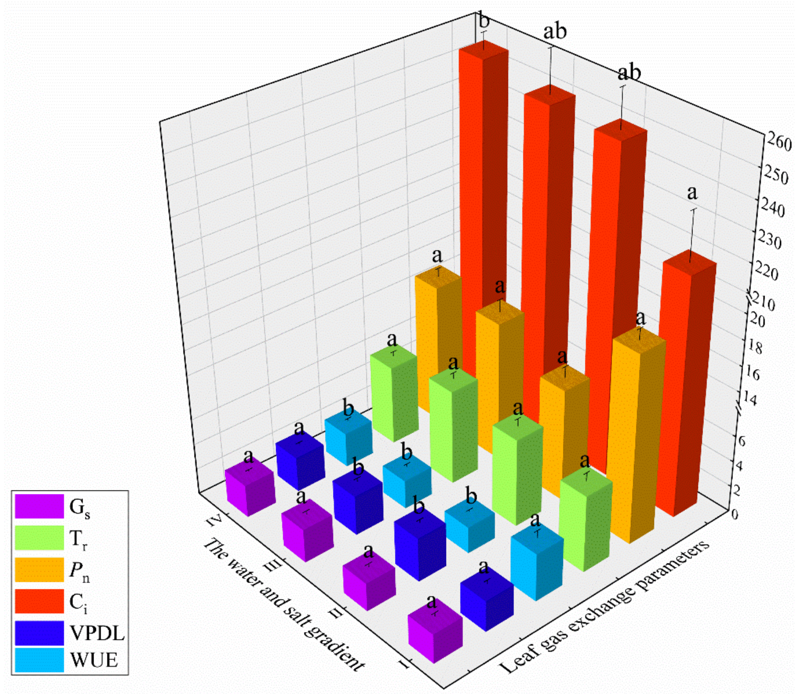

Figure 2. Variations of leaf gas exchange parameters of *Haloxylon ammodendron* under the water and salt gradient (PPFDi: 1500 μmol·m^{-2}·s^{-1}). For the convenience of drawing, G_s is enlarged by 10 times; different lowercase letters indicate significant differences between the same traits under different water and salt gradients ($P < 0.05$); G_s: stomatal conductance; T_r: transpiration rate; P_n: net photosynthetic rate; C_i: intercellular CO_2 concentration; VPDL: vapor pressure deficit; WUE: water use efficiency.

3.4. Relationship between Morphological Characters and Photosynthetic Physiology

The results of the DCA (Detrended Correspondence Analysis) analysis showed that the maximum length of the four axes in this study was 0.395, which is less than 3, in accordance with the linear model. Therefore, the RDA method was used to explore the relationship between the morphological characteristics of *Haloxylon ammodendron* and the gas exchange parameters. The results of the RDA analysis showed that sorting axes 1 and 2 explained 69.8% and 25.6%, respectively, of the relationship between morphological characters and gas exchange parameters (Table 6), and the relationship between morphological characters and gas exchange parameters could be fully explained by using the data of the first two axes.

Table 6. Redundancy analysis (RDA) analysis results of morphological indexes and gas exchange parameters of *Haloxylon ammodendron.*

Item		Axis1	Axis2
Eigenvalues		0.074	0.027
Morphology-photosynthetic correlations		0.328	0.354
Cumulative percentage variance	Morphological data	7.4	10.2
	Morphology-photosynthetic relationship	69.8	95.4
Sum of all eigenvalues		1	
Sum of all canonical eigenvalues		0.11	

In the RDA analysis results for *Haloxylon ammodendron* morphological indexes and gas exchange parameters (Table 7, Figure 3), the interpretation rate of the morphological indexes was ranked as LDMC > SLA > CA > H > LA > LT > BD, and LDMC significantly affected gas exchange parameters ($P < 0.1$). The first sort axis basically reflects the changes in LDMC, SLA, CA, and H, and the correlation coefficients with the first sort axis were

0.2392, 0.2008, 0.1815, and 0.1606, respectively. In summary, the morphological indexes that mainly affect the gas exchange parameters of *Haloxylon ammodendron* were LDMC, SLA, and CA. LDMC was negatively correlated with photosynthetic rate, while SLA and CA were positively correlated with photosynthetic rate.

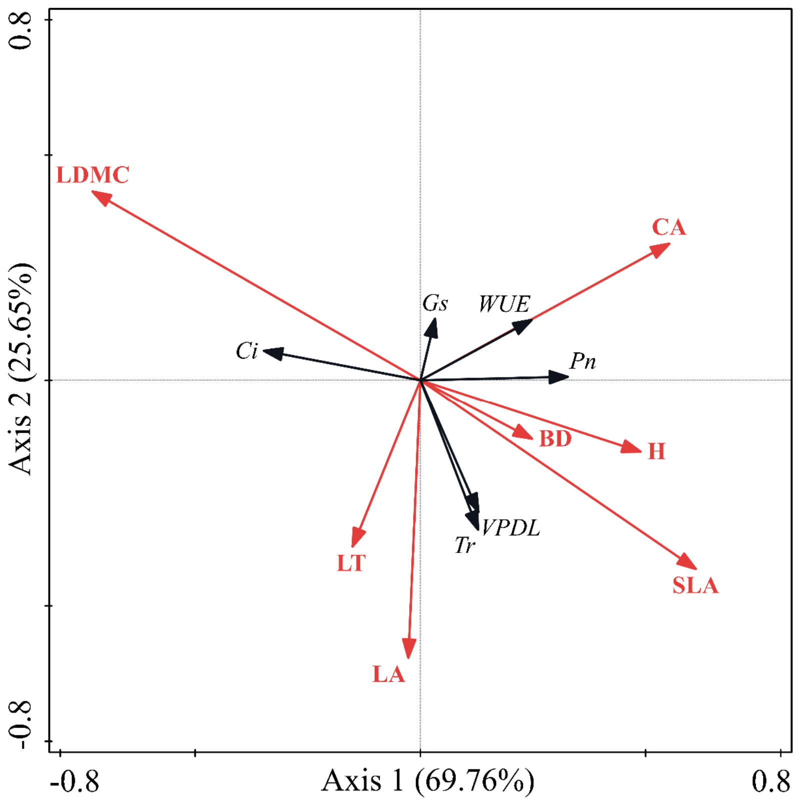

Figure 3. RDA ordination between morphology index and gas exchange parameters of *Haloxylon. ammodendron*. The black line indicates gas exchange parameters, while the red line indicates morphological characters; the included angle between gas exchange parameters and morphological characters is acute, indicating that they are positively correlated, while obtuse angles indicate negative correlations.

Table 7. The correlation coefficients from the RDA between morphology index and gas exchange parameters of *Haloxylon ammodendron* (first two axes).

Item	Axis 1	Axis 2	Explained (%)	*P*
LDMC	−0.2392	−0.1482	4.4	0.07
SLA	0.2008	0.1484	3.3	0.134
CA	0.1815	0.1074	2.5	0.212
H	0.1606	−0.0564	1.9	0.288
LA	−0.0088	−0.2178	1.1	0.5
LT	−0.0495	−0.1307	0.7	0.648
BD	0.0813	−0.0461	0.5	0.752

Bold indicates significance ($P < 0.1$).

4. Discussion

Changes in environmental conditions will affect the growth of plants. The results showed that the soil salt content was higher under gradient I (Table 2), but *Haloxylon ammodendron* plants grew well, and the basal diameter, plant height, and crown area were significantly higher than in gradients II, III, and IV (Table 3) indicating that *Haloxylon ammodendron* could cope with salt stress. However, when *Haloxylon ammodendron* suffered from drought stress, its morphological indexes showed a downward trend, similar to the research results of previous studies [19,20]. One possible reason is that under drought stress, the net photosynthetic rate of plants decreases, and the photosynthetic products are affected, thus limiting plant growth. At the same time, some studies have shown that too low phosphorus in the soil will lead to slow growth of plants, thereby affecting plant height and basal diameter [21]. The leaf is the main organ for photosynthesis and respiration. When the environmental conditions change, the leaf morphology is more sensitive in its response [22,23]. Some studies suggest that the ability of plants to obtain light resources and adapt to different habitats can be reflected by specific leaf area and dry matter content of leaves [24,25], and some researchers believe that specific leaf area of perennial plants is negatively correlated with dry matter content of leaves [26].

In this study, LDMC increased with the decrease of water and salt content, while the specific leaf area decreased, indicating that there was a negative correlation between these factors. The results of the RDA showed that LDMC and SLA were morphological indexes that affected the gas exchange parameters of *Haloxylon ammodendron*, indicating that leaf traits were closely related to photosynthetic parameters. Du found that a larger specific leaf area indicated a greater light catching area per unit leaf biomass, and thus could increase the photosynthetic capacity of plants [27]. In gradient I, SLA was significantly higher than that of other gradients, and the photosynthetic rate was the highest among all gradients. The main reasons are as follows: owing to the favorable soil conditions, the plants were relatively lush, and the shading phenomenon among the neighbors generated fierce light competition among the plants. To maximize the carbon assimilation rate, the specific leaf area of *Haloxylon ammodendron* increased accordingly, thereby increasing the light-catching area and the net photosynthetic rate. However, while increasing the specific leaf area, plants need to sacrifice leaf thickness and quality, resulting in thinner leaves and lower dry matter content [28]. In other words, when the growing environment is dry and resources are scarce, *Haloxylon ammodendron* can adapt to the environment by reducing the specific leaf area; when growing in a resource-rich environment, the specific leaf area is higher, and therefore *Haloxylon ammodendron* reduces the chance of losing water under drought stress by adjusting its leaf morphological characteristics to maintain a relatively stable water content. This illustrates how a strong water retention capacity ensures the water supply required by plants for their growth and physiological processes. Other studies have also reached similar conclusions [29,30]. Previous studies have shown that the soil nutrient content can significantly affect the leaf area of plants in controlled experiments [31], but in the present study, there was no significant difference between leaf area and leaf thickness of *Haloxylon ammodendron* in the four gradients, which may be due to the long-term evolution and adaptation to the local environment.

Under drought stress, there are usually two reasons for the decline of photosynthetic rate of plants, namely, "stomatal limitation" and "non-stomatal limitation" [19,20,32]. The former states that the decrease of stomatal conductance leads to the obstruction of CO_2 entering leaf cells, thus reducing the photosynthetic rate. The latter suggests that the loss of water leads to a decrease in the carboxylation ability of mesophytic cells or an insufficient homogeneity of the electron transport chain, which in turn leads to a decrease in the photosynthetic rate. Thus, when the photosynthetic rate is decreased, if the intercellular CO_2 concentration and stomatal conductance are decreased, the net photosynthetic rate will mainly be affected by "stomatal limitation." If the decrease in photosynthetic rate is accompanied by an increase in intercellular CO_2 concentration, it is thought to be mainly affected by "non-stomatal limitation" [33,34]. In this study, P_n of *Haloxylon ammodendron* in gradient I was significantly higher than that in other gradients, while C_i and G_s were lower than those in other gradients, indicating that the photosynthetic rate of *Haloxylon ammodendron* in gradient I was mainly affected by stomatal limitation. The increase of P_n in gradients II, III, and IV was accompanied by the increase of C_i and G_s, indicating that the photosynthetic rate was mainly affected by "non-stomatal limitation." Brugnoli found that soil salinity was negatively correlated with stomatal conductance of plants, and leaf stomatal conductance decreased with the increase of soil salinity, leading to a sharp decrease in CO_2 entering plants. This further suggests that the photosynthetic rate of *Haloxylon ammodendron* in gradient I was mainly affected by stomatal limitation. It is worth noting that the net photosynthetic rate of *Haloxylon ammodendron* increased slightly with the decrease of water content in gradients II, III, and IV. One possible reason is that the decrease of soil salt content alleviated the negative effects of drought stress on photosynthesis.

In arid areas, as an important indicator of plant gas exchange, WUE is closely related to the environment [35], and the greater its value, the higher the water use efficiency of plants. Different gradients showed different water use strategies: in gradient I, *Haloxylon ammodendron* had higher water use efficiency and lower transpiration rate, indicating that it could make full use of limited water, consistent with the relatively good growth under this gradient; however, in gradients II, III, and IV, the drought stress deepened, leading to a significant decrease in photosynthetic rate and water use efficiency, especially in gradient II.

The maximum net photosynthetic rate of leaves reflects the maximum photosynthetic capacity of plants. Previous studies have shown that the maximum net photosynthetic rate of plants decreases gradually with the aggravation of drought stress [36]. Our results showed that with the decrease of water content, the maximum net photosynthetic rate of *Haloxylon ammodendron* in gradients II, III, and IV showed a slight upward trend, further confirming that *Haloxylon ammodendron* in this gradient was more affected by water and salt stress. AQY is an index used to characterize the light energy conversion efficiency of plant leaves and the ability to use weak light for photosynthesis [37]. The higher the value, the stronger the ability. The light compensation point is an indicator of plants' ability to utilize low light. The smaller the value, the stronger the ability to utilize low light [38]. In this study, AQY and the maximum net photosynthetic rate showed the same change rule, while the light compensation point was opposite, indicating that the photosynthetic capacity of *Haloxylon ammodendron* in gradient I was stronger than that in other gradients.

The content of soil nutrients will affect plant growth and development as well as plant metabolism and physiology [39]. For example, as an important component of plant chlorophyll and photosynthesis-related enzymes, a lack of nitrogen will lead to a decrease of leaf area and the obstruction of chlorophyll synthesis, which will in turn affect the photosynthetic rate and the formation of photosynthetic products [40]. However, phosphorus can regulate photosynthesis and carbohydrate metabolism of plants. Some studies have shown that with the increase of phosphorus content, the net photosynthetic rate and water use efficiency show clear increasing trends [41]. In this study, the contents of total nitrogen and total phosphorus in the soil of gradient I were significantly higher than those of other gradients that provided better soil conditions for photosynthesis. The photosynthetic rate of *Haloxylon ammodendron* in gradients II, III, and IV was significantly lower than that in gradient I, and water use efficiency showed a clear upward trend.

5. Conclusions

(1) The growth of *Haloxylon ammodendron* is subject to water and salt stress. With the decrease of soil water and salt content, the plant height, base diameter, crown area and specific leaf area of *Haloxylon ammodendron* all showed downward trends to varying degrees, while the dry matter content of leaves gradually increased.

(2) Soil water and salt content can affect the photosynthesis of *Haloxylon ammodendron*, and the factors limiting the photosynthetic ability are different under different gradients. The photosynthetic rate of *Haloxylon ammodendron* in gradient I was much higher than that in other gradients; the photosynthetic rate in gradient I was mainly affected by "stomatal limitation," while the rates in gradients II, III, and IV were mainly affected by "non-stomatal limitation."

(3) In arid areas, *Haloxylon ammodendron* has its own special survival strategy and leaf construction mode. When the soil conditions are good, to cope with the light competition phenomenon caused by the density of plants, *Haloxylon ammodendron* displays a leaf construction mode with high specific leaf area. This morphology mitigates insufficient light energy absorption of plants in shaded environments and maximizes

the photosynthetic income. When the soil conditions worsen, *Haloxylon ammodendron* chooses the leaf construction mode with low specific leaf area, thereby realizing the optimal distribution of carbon assimilation products and the dissipation of solar energy by the leaves.

Author Contributions: Conceptualization, G.L. and D.H.; formal analysis, D.H., L.J. and H.W.; investigation, D.H. and Y.Q.; writing—original draft, D.H.; writing—review & editing, G.L., F.Y. and H.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Natural Science Foundation of China (no. 31560131).

Acknowledgments: The authors thank LetPub for their assistance with English language and grammatical editing.

Conflicts of Interest: The authors declare no conflict of interest.

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