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The Influence of Sodium Salt on Growth, Photosynthesis, Na^+/K^+ Homeostasis and Osmotic Adjustment of *Atriplex canescens* under Drought Stress

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Abstract: *Atriplex canescens* is widely cultivated as drought and salt-tolerant fodder in arid regions of Northwest China, which is used for photoremediation of degraded land and soil and water conservation. To explore the growth performance of *A. canescens* when exposed to drought and salt stress, seedlings were treated with a range of drought stress (WC1: 75 ± 3.6%, WC2: 49 ± 2.9% and WC3: 27 ± 2.5% of soil water content) and the corresponding drought stress with additional sodium salt supplementation ($NaCl:Na_2SO_4 = 1:1$ with the total concentration of Na^+ set to 150 mM). The findings of this paper indicated that moderate sodium salt could stimulate the growth of *A. canescens* and effectively alleviate the deleterious impact of drought stress by increasing the turgor potential (ψt) and relative water content (RWC) and decreasing the leaf water osmotic potential (ψs). Furthermore, the photosynthetic capacity was improved and the negative effects of drought stress on photosystem II (PSII) were mitigated. The extra 150 mM sodium salt also markedly increased the contribution of Na^+ to ψs and the contribution of betaine to ψs. In summary, these results indicate that *A. canescens* can adapt to drought stress by accumulating enough Na^+ for osmotic adjustment (OA). Additionally, this paper is aimed to provide a fundamental basis for the utilization and cultivation of *A. canescens* as a favored pasture crop in the Qaidam basin, thus increasing the ecological and environmental benefits for arid regions worldwide.

Keywords: *Atriplex canescnes*; drought stress; sodium ion; osmotic adjustment; chlorophyll fluorescence

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1. Introduction

The issue of drought not only influences the global ecological environment, but also severely constrains the development of agroforestry and livestock production worldwide [1,2]. In arid and semiarid regions, extreme drought frequently occurs and leads to the soil salt concentration in the remanent soil solution; thus, drought and salt stress frequently co-occur [3], which can cause dehydration and toxication of plant tissues [4,5]. Some halophytes have developed a variety of tolerance mechanisms under drought and salt stress to protect themselves from harsh environments [6,7]. It is important to investigate the physiological mechanisms of drought and salt-resistant plants and the limits and traits associated with drought stress combined with some extent of salinity. The majority of current studies separately explore the two stresses, and only a few investigations have noticed their interactions. Drought and salinity are generally considered additive stress factors for plants [3], but are used as individual elements to reduce the crop yield in some agricultural models. Therefore, understanding the drought resistance mechanisms of halophytes could be of great importance in agricultural development and environmental remediation in arid land [8].

Osmotic adjustment (OA) is an important pattern of metabolism that can help halophytes with drought and salt stress [7,9,10]. OA involves the accumulation of solutes in plant cells under low water and salt conditions, and these solutes are often comprised of regulators such as organic solutes and inorganic ions [11]. Betaine and proline are two typical organic solutes, that are usually considered to contribute to OA in plants, while inorganic ions, especially K^+, are generally considered to have a great influence on the OA of plants under drought and saline conditions [12,13]. Generally, ionic imbalance occurs resulting from the superfluous accumulation of Na^+ and Cl^- and lower uptake of other mineral nutrients, such as Ca^{2+} and Mg^{2+}. However, some researchers have shown that plants growing in drying soil with different concentrations of salt have a complicated response mechanism and that moderate soil salt can alleviate drought stress in these species [14]. For example, in a previous study [15], researchers found that saline water had a protective effect on a variety of crop yields with deficit irrigation. Others [16,17] have studied *Sesuvium portulacastrum* subjected to water deficit with salinity and found that NaCl improves plant growth under water stress induced by mannitol, and the relative water content (RWC) and plant growth were restored by releasing water stress in the presence of NaCl. Additionally, the biomass production of *A. hortensis* and *A. lentiformis* was proven to be improved by NaCl via promoting water use efficiency (WUE) in dry soil [18]. The positive roles of NaCl in the drought resistance of *Zygophyllum xanthoxylum* might be due to the ability of plants to accumulate a high concentration of Na^+ and absorb the excessive Na^+ for OA, which was coupled with an improvement in leaf hydration and photosynthetic activity [19,20]. Photosynthesis is an important process that can reveal the impacts of drought and salt stress on plants. Except for the traditional parameters, chlorophyll fluorescence also can be used as a sensitive and effective tool for evaluating the impacts of drought and salt stress. Therefore, the drought and salinity stress damage to plants in the process of electron transportation in the light reaction of photosynthesis could be evaluated using chlorophyll fluorescence kinetics [21]. According to Guo and Zhao, the reduction of the photosystem II (PSII) reaction center (RC) could be suggested by the kinetics, including the fluctuations of initial fluorescence (F_o) and maximal fluorescence (F_m) as well as the maximal quantum yield of PSII photochemistry (F_v/F_m), the effective quantum yield of PS II photochemistry (F_v'/F_m'), the actual PSII efficiency (Φ_{PSII}), the photochemical quenching coefficient (qP), and the nonphotochemical quenching coefficient (qN) [22,23]. Moreover, the O-J-I-P curve could also reflect the changes in plant photosynthetic apparatus under the influence of drought and salt stress [24].

The C4 perennial evergreen shrub *Atriplex canescens* (Chenopodiaceae) acclimatized to arid and saline environments in North America was introduced to China in 1990 [25]. This plant can be extensively utilized for remediation and afforestation in eroded soil and saline soil and for sand fixation attributed to its eminent tolerant ability to drought and salt [26]. Furthermore, this species can also be a remarkable fodder for livestock in arid regions due to its abundant nutritional properties. Previous studies have shown that *A. canescens* has a strong ability to acclimatize to drought, salinity, and cold environments [27]. According to one study [28], the tolerant mechanism of *A. canescens* is achieved through Na^+ uptake for OA, and the degree of stress on plants in dry soil would be aggravated rather than mitigated. Previous investigations examined the impact of either drought or salt stress on *A. canescens*. However, it has not been thoroughly investigated whether photosynthesis, Na^+/K^+ homeostasis and OA mechanisms, especially chlorophyll fluorescence, are involved in this species under drought and salt combined stress.

Therefore, to elucidate the physiological characteristics of *A. canescens* under drought and salt stress and the interactions of these stresses, we evaluated the impacts of salt and water stress on *A. canescens* on indices related to growth, photosynthesis, ion homeostasis and OA under controlled experimental conditions.

2. Materials and Methods

2.1. Plant Growth Conditions and Stress Treatments

Seeds of *A. canescens* were collected from the Research Institute of Forestry, Qinghai Academy of Agriculture and Forestry. The site is located at Nuomhon Farm, Qinghai Province, China (96°15′–96°35′ E, 36°20′–36°30′ N; elevation 2790 m), where the average annual temperature, the average annual rainfall and the annual evaporation are 4.9 °C, 43.5 mm, and 2849.7 mm, respectively. After treated with H_2SO_4 and distilled water, the seeds were germinated in a greenhouse in a dark environment for 8 days. The seeds were cultured to seedlings. In April 2016, 5-week-old *A. canescens* seedlings were individually transplanted into igelite pots (18 cm × 15 cm × 10 cm, 6 plants per pot) containing local soil and kept in a sunlight greenhouse. The chemical properties of the substrate are shown in Table 1. The ring samples method was used to determine the field capacity and bulk density of the substrate, and the values were 25.3 ± 1.1% and 1.11 ± 0.08 g/cm^3. The potted plant was sufficiently irrigated with half-strength Hoagland solution [19] to maintain 75% of field water capacity at 2-day intervals. The temperature in the greenhouse ranged from 27.5 to 19.0 with a 16 h photoperiod, 8 h dark time, 300–800 $\mu mol\ m^{-2}s^{-1}$ of photosynthetically active radiation (PAR) at 800 and relative humidity of 65% ± 2.5.

Table 1. Some chemical properties of soil filled into the pots. Values are means from six soil pots ± SE (*n* = 18).

Water Soluble Ion Concentration (μmol g^{-1})				**Changeable Ion Concentration (μmol g^{-1})**				**Available P (μmol g^{-1})**	**Available N (μmol g^{-1})**	**pH**
Na^+	**K^+**	**Ca^{2+}**	**Mg^{2+}**	**Na^+**	**K^+**	**Ca^{2+}**	**Mg^{2+}**			
7.4 ± 0.5	2.5 ± 0.2	1.6 ± 0.1	1.3 ± 0.1	3.4 ± 0.3	3.6 ± 0.3	0.9 ± 0.0	0.7 ± 0.0	0.6 ± 0.0	0.07 ± 0.0	8.7 ± 0.7

Five-week-old seedlings with similar heights and stem diameters were chosen and divided into seven groups for further experiments. Each group had three replications. One group continued to be cultivated in aboveground soil to measure the growth indices, and the other six groups were subjected to stress treatment. The other 6 groups were evenly divided into 3 different soil relative water content (SRWC) regimes. We used an LNW-50A neutron probe (CAS, Nanjing, Jiangsu, China) to obtain and maintain the water content of the seedlings. The soil moisture gradients were obtained through a modified 1/2 Hoagland nutrient solution addition and natural water consumption. After watering the pot to saturation, the variations in the SRWC were in line with the D-optimum law, reflecting that the potted plants endured a successive extent of water stress via evapotranspiration; the SRWC was 75 ± 3.6% (WC1), 49 ± 2.9% (WC2) and 27 ± 2.5% (WC3). WC1 treatment is defaulted to be the control group. Based on the SRWC value, we calculated the mass of salt that needed to be dissolved in the nutrient solution. The SRWC values were maintained by adding the corresponding nutrient solution with or without a mixture of NaCl and Na_2SO_4 (NaCl:Na_2SO_4 = 1:1 with the total concentration of Na^+ set as 150 mM) to simulate the salt composition and pH in most saline soil in the Qaidam basin of Qinghai Province. The seedlings were treated with half-strength Hoagland solution involving increased 50 mM salt at 17:30–18:30 every day and the other groups were irrigated with the nutrient solution at the same time to sustain the SRWC. The pH of the soil progressively increased and stabilized at 8.3–9.6 after 20 days. All the groups were classified as follows: SRWC of 75 ± 3.6% without additional NaCl and Na_2SO_4 (WC1); SRWC of 75 ± 3.6% with additional NaCl and Na_2SO_4 (WC1+S); SRWC of 49 ± 2.9% without additional NaCl and Na_2SO_4 (WC2); SRWC of 49 ± 2.9% with an additional 150 mM NaCl and Na_2SO_4 mixed salt (WC2+S); SRWC of 27 ± 2.5% without additional NaCl and Na_2SO_4 (WC3); and SRWC of 27 ± 2.5% with an additional 150 mM NaCl and Na_2SO_4 mixed salt (WC3+S). The growth, photosynthesis, chlorophyll fluorescence, Na^+ and K^+ homeostasis and physiological parameters were obtained after 20 days.

2.2. Determination of Physiological Indices

Leaves of seedlings were collected to assess the fresh weight (FW) and then soaked in deionized water for 24 h at 4 °C overnight in the dark to determine the leaf turgid weight (TW), and finally dried at 80 °C for 48 h to determine the dry weight (DW). Thirty medial leaves were collected from each plant per treatment. The leaf RWC was calculated with the formula described by [10]. And the relative growth rate (RGR) was determined according to a previously reported method [7,29].

$$\mathrm{RWC}\ (\%) = (100 \times (\mathrm{FW} - \mathrm{DW}))/(\mathrm{TW} - \mathrm{DW}) \tag{1}$$

$$\mathrm{RGR} = (\ln \mathrm{DW}_0 - \ln \mathrm{DW}_1)/\mathrm{D} \tag{2}$$

where DW_0 means the final DW, DW_1 means the initial DW, and D means the duration of the stress treatment.

2.3. Measurement of Photosynthetic Parameters

The net photosynthetic rate (P_n), stomatal conductance (g_s) and transpiration rate (T_r) were measured on fully expanded third blades using a portable photosynthesis system LI-6400 (LI-COR Biosciences, Lincoln, NE, USA) with a light intensity of 1000 µmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$ (saturated light intensity), a CO_2 concentration of 400 µmol mol^{-1} and a leaf temperature of 28 °C. All parameters were measured between 8:00 a.m. and 6:00 p.m., and every two hours the parameters were measured during this period. The *WUE* was calculated as $WUE = P_\mathrm{n}/T_\mathrm{r}$. Leaf areas were determined using a photo scanner (CANON CS4600F, CANON, Inc. Tokyo, Japan). All the treatments and repetitions were measured almost in the same position of the blades.

2.4. Measurement of Chlorophyll Fluorescence Kinetics

F_o, F_m, and F_v were measured with a portable fluorometer (Hand PEA, Hansatech, Britain) between 6:00 and 7:00 in the morning after adaptation for a night in the dark (He et al., 2019). The parameters were measured under the leaf temperature of 28 °C and CO_2 concentrations of 500 µmol mol^{-1} [30]. F_s, F_o', and F_m' were determined to calculate the other variables, including $F_\mathrm{v}/F_\mathrm{m}$, $F_\mathrm{v}'/F_\mathrm{m}'$, Φ_PSII, qP and qN [31]:

$$Fv/Fm = (Fm - Fo)/Fm \tag{3}$$

$$Fv'/Fm' = \left(Fm' - Fo'\right)/Fm' \tag{4}$$

$$\Phi_\mathrm{PSII} = \left(Fm - Fs\right)/Fm' \tag{5}$$

$$qP = \left(Fm' - Fs\right)/\left(Fm' - Fo'\right) \tag{6}$$

$$qN = 1 - \left(Fm' - Fo'\right)/\left(Fm - Fo\right) \tag{7}$$

2.5. Measurement of Leaf Water Potential-Related Parameters

The leaves at the same position of each treatment were rinsed with deionized water after blotting the surface water and then immediately frozen in liquid nitrogen for 20 min. The leaves water potential (ψw) was determined with a PSYPRO dew point water potential meter (C-52 Chamber, WESCOR Inc., Logan, UT, USA). The leaves were used to extract the sap by a 1 mL syringe after thawing and 50 µL supernatant was collected after centrifugation at 10,000× *g* at 25 °C for 2 min. The leaf osmotic potential (ψs) was measured by a cryoscopic osmometer at 25 °C (Osmomat-030, Gonotec Gmb H, Berlin, Germany). The leaf turgor potential (ψt) was calculated with the following formula [19]):

$$\psi\mathrm{w} = \psi\mathrm{s} + \psi\mathrm{t} \tag{8}$$

2.6. Determination of Ion Contents

The Na^+ or K^+ concentrations in tissues were determined following a previously described method [10]. All the samples were rinsed with deionized water and dried in an oven at 80 °C for 72 h to obtain the DW. Then, the samples were extracted with 100 mM acetic acid under 90 °C for 2 h to obtain the contents of Na^+ and K^+ from tissues. After the water bath, cooling, and filtering, cation accumulation was conducted with a flame spectrophotometer (2655-00, Cole-Parmer Instrument Co., Vernon Hills, IL, USA).

2.7. Determination of Betaine and Free Proline

To determine the betaine, leaves from seedlings were dried under 80 °C for 24 h, and then finely grounded. An amount of 1 mL of 80% methanol was mixed with the dried and ground samples (0.2 g) and then the mixture was shaken in a 60 °C water bath for half an hour. After shaking, the mixture was centrifugated at 11,000× *g* at 25 °C for a quarter to harvest the extraction. Then, 0.35 mL of Reinecke salt-saturated solution was added into the extracted solution (0.25 mL) to react for 2 h at 4 °C. After centrifugation at 10,000× *g* at 25 °C for 15 min, the supernatant was discarded and the precipitate was washed using 0.3 mL of 99% ether. The precipitate was then dissolved in 70% acetone (1 mL). At last, a spectrophotometer (UV-6100PCS; Mapada Instruments, Co., Ltd., Shanghai, China) was used to measure the absorbance at 525 nm. And a standard sample in the kit was used to calculate the betaine content.

Proline in leaves was measured with 1 mL of 5% salicylic acid homogenized to 0.1 g fresh leaf and then the mixture was shaken in boiling water for 10 min to obtain the extraction. The supernatant was centrifugated at 10,000× *g* at 25 °C for 10 min and then collected. After heating the mixture of the supernatant (0.5 mL) and glacial acetic acid (0.5 mL) in boiling water for half an hour, 1 mL of toluene was added, and the mixture was shocked for 30 s. At last, a spectrophotometer was used to measure the absorbance at 520 nm. The concentration of free proline was calculated with the following equation:

$$y = 0.0521x - 0.0021 \tag{9}$$

where x means free proline concentration, μg/mL; y means OD value.

2.8. Determination of the Contributions of Solutes to Leaf ψs

The calculated osmotic potential (COP) values of solutes were calculated by the following equation:

$$\psi s = -nRT \tag{10}$$

where n represents the solute molecule concentration, R = 0.008314 and T = 298 [32].

The contribution rate of each solute to the leaf ψs (CR) was calculated as follows:

$$CR = \psi ss/\psi sl \tag{11}$$

where ψss and ψsl are the solute COP and leaf ψs, respectively [32].

2.9. Statistical Analysis

SPSS statistical software (Ver. 19.0, SPSS, Inc., Chicago, IL, USA) was used to perform the statistical analysis. One-way analysis of variance (ANOVA) was conducted to test the impacts of stress on the parameters. Duncan's multiple range test was used to reveal the significant differences among means at $p < 0.05$. All the acquired data were shown in the form of an average and standard error (SE) ($n \geq 3$).

3. Results

3.1. Growth Performance

After treatment with various water contents or without salt for 20 days, the results indicated that compared to WC1, drought stress (WC2 and WC3) significantly suppressed the plant height, ground diameter, dry mass, fresh mass and RGR of *A. canescens* seedlings, and the extent of inhibition was most conspicuous under WC3. The growth was found to be stimulated significantly after the addition of 150 mM mixed salt solution (WC1+S, WC2+S, and WC3+S), which may mitigate the restraint of water stress. The data showed that compared to WC1 treatment, WC1+S increased the plant height, ground diameter, fresh mass, dry mass and RGR of *A. canescens* seedlings by 15.30, 11.2, 12.78, 14.13 and 14.06%, respectively. Compared to the WC1 treatment, under the WC2 and WC3 treatments for 20 days, the plant height, ground diameter, fresh mass, dry mass and RGR of *A. canescens* seedlings were significantly reduced by approximately 24.59, 14.51, 22.51, 20.50 and 21.47% and 44.81, 37.09, 47.58, 46.26 and 37.06%, respectively. However, the growth performance distinctively improved under WC2+S and WC3+S compared to WC2 and WC3. The plant height, ground diameter, fresh mass, dry mass and RGR increased by 15.21, 18.87, 10.73, 13.59 and 11.99% under the WC2+S treatment and by14.85, 17.95, 19.57, 14.94 and 15.26% under the WC3+S treatment in comparison with the corresponding treatments (Table 2).

Table 2. Plant height, ground diameter, dry mass, fresh mass and relative growth rate (RGR) of *A. canescens* seedlings grown under different treatments for 20 days. Values are means ± SE (n = 18) and different letters in columns indicate significant differences at $p < 0.05$ (Duncan's multiple range test).

Treatments	Plant Height (cm)	Ground Diameter (cm)	Dry Mass (g)	Fresh Mass (g)	RGR × 10^3 (g kg^{-1} d^{-1})
WC1	18.3 ± 0.96 b	0.62 ± 0.08 c	36.1 ± 2.23 b	365.5 ± 12.11 b	16.35 ± 0.79 b
WC1+S	21.1 ± 0.67 a	0.69 ± 0.07 a	41.2 ± 1.39 a	412.2 ± 10.35 a	18.65 ± 0.89 a
WC2	13.8 ± 0.88 d	0.53 ± 0.08 d	28.7 ± 1.18 d	283.2 ± 13.15 d	12.84 ± 0.82 d
WC2+S	15.9 ± 0.52 c	0.63 ± 0.06 b	32.6 ± 2.61 c	313.6 ± 12.39 c	14.38 ± 0.69 c
WC3	10.1 ± 0.31 f	0.39 ± 0.05 f	19.4 ± 1.33 f	191.6 ± 10.31 f	10.29 ± 0.81 f
WC3+S	11.6 ± 0.12 e	0.46 ± 0.06 c	22.3 ± 1.98 e	229.1 ± 16.11 e	11.86 ± 0.59 e

3.2. Photosynthetic Capacity and Water Use Efficiency (WUE)

As shown in Figure 1, the photosynthetic capacity of *A. canescens* seedlings significantly decreased under WC2 and WC3 treatments. However, it was partially restored with salt supplementation. Under the WC2 treatment for 20 days, P_n, g_S and T_r decreased by 31.48, 43.98 and 9.7%, respectively (Figure 1). When the seedlings were under the WC3 treatment, the photosynthetic capacity was substantially inhibited. The P_n, g_S and T_r decreased by 48.28, 56.27 and 55.43% (Figure 1), respectively, compared to the WC1 treatment. However, the photosynthetic capacity was somewhat restored with the addition of a 150 mM salt solution. The P_n increased by 18.65, 20.27 and 11.76% in the WC1+S, WC2+S and WC3+S treatments compared to each corresponding water treatment, respectively (Figure 1). In comparison with each water treatment, g_S and T_r in the WC1+S, WC2+S and WC3+S treatments showed obvious increasing trends of 21.56, 24.58 and 9.13%, and 44.57, 5.69 and 73.08%, respectively (Figure 1). Correspondingly, the plant WUE showed a sharp decrease of 17.93 and 35.43% in the WC1 and WC3 treatments compared to the WC1+S and WC3+S treatments; the plant WUE for the WC2+S treatment markedly increased by 13.79% compared to the WC2 treatment (Figure 1).

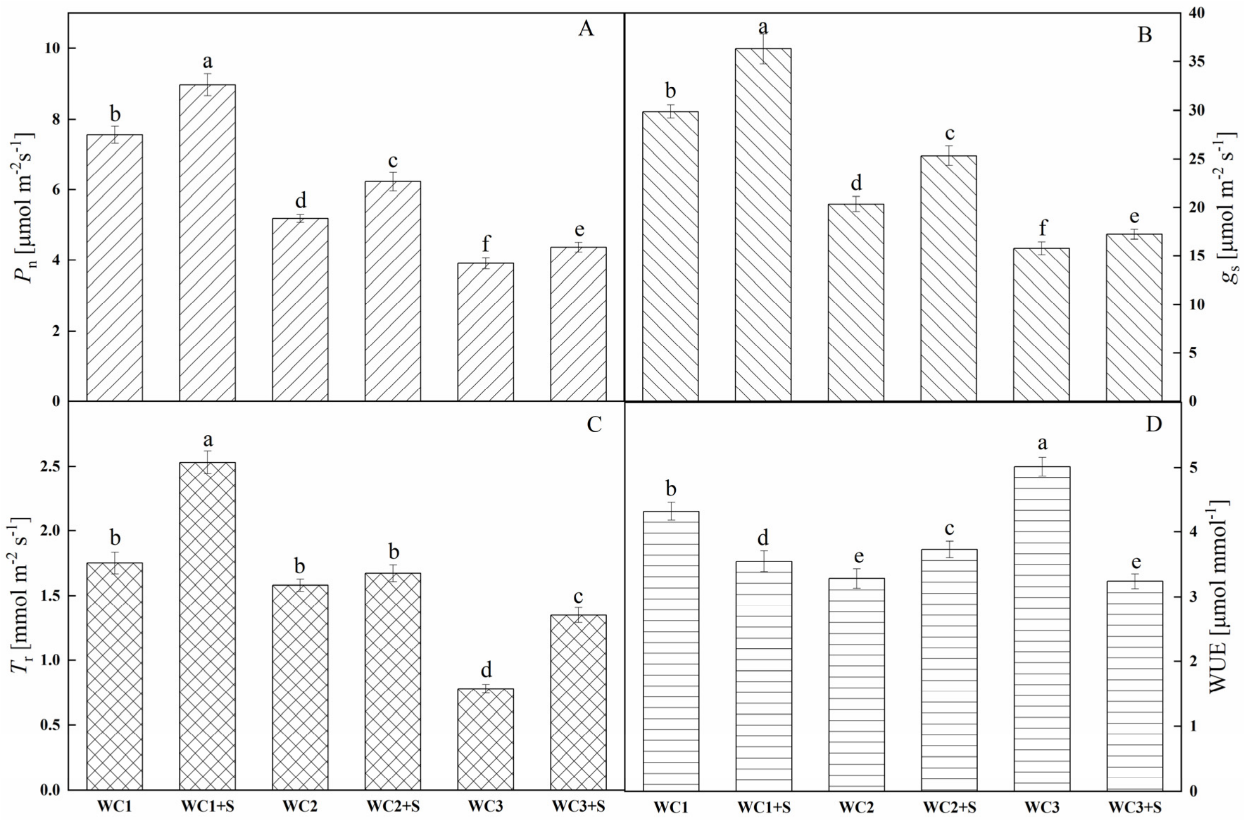

Figure 1. Net photosynthetic rate (P_N) (**A**), stomatal conductance (g_S) (**B**), transpiration rate (T_r) (**C**), and water use efficiency (WUE) (**D**) of *A. canescens* seedlings under different treatments for 20 days. Values are means ± SE (n = 18) and bars indicate SE. In each column, different letters in the same curve indicate significant differences at $p < 0.05$ according to Duncan's test.

3.3. Chlorophyll Fluorescence

Figure 2 showed that the chlorophyll fluorescence of *A. canescens* presented an obvious O-J-I-P curve in different treatments. The recorded transient characteristics were found to increase rapidly at J and I points, based on a modified graph containing the phases in O-J-I-P [33]. An obvious increase was found in the F_v/F_m, F_v'/F_m', Φ_{PSII} and qP of *A. canescens* under different water treatments when compared with the results for the corresponding treatment with an additional 150 mM salt, while qN showed a contrasting trend (Figure 3). Moreover, drought stress induced a pronounced decrease in F_v/F_m, F_v'/F_m', Φ_{PSII} and qP, while an augment in qN (Figure 3). The data were normalized in the 'radar' chart, and the magnitudes of most kinetics were depicted to qualify the PSII function. It is clearly illustrated that most kinetics were increased with the additional salt solution (WC1+S, WC2+S, and WC3+S) in comparison to the corresponding water treatment (WC1, WC2, and WC3), while ETo/RC and TRo/RC were decreased (Figure 4A–C). The downregulation of F_o, F_m, F_v, F_v/F_m and F_v/F_o was observed under drought stress, whereas upregulation of the other kinetics was observed when *A. canescens* seedlings were under drought conditions (Figure 4D).

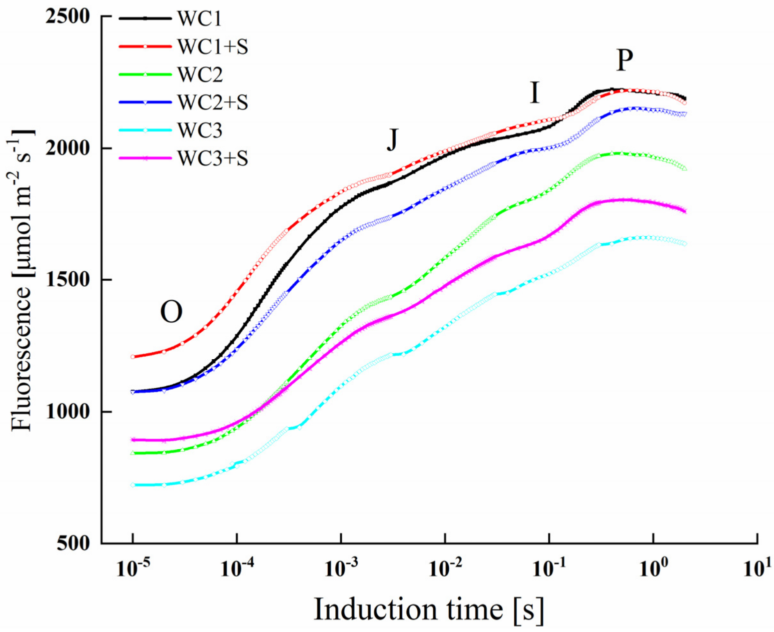

Figure 2. The O-J-I-P curve of *A. canescens* seedlings under different treatments for 20 days.

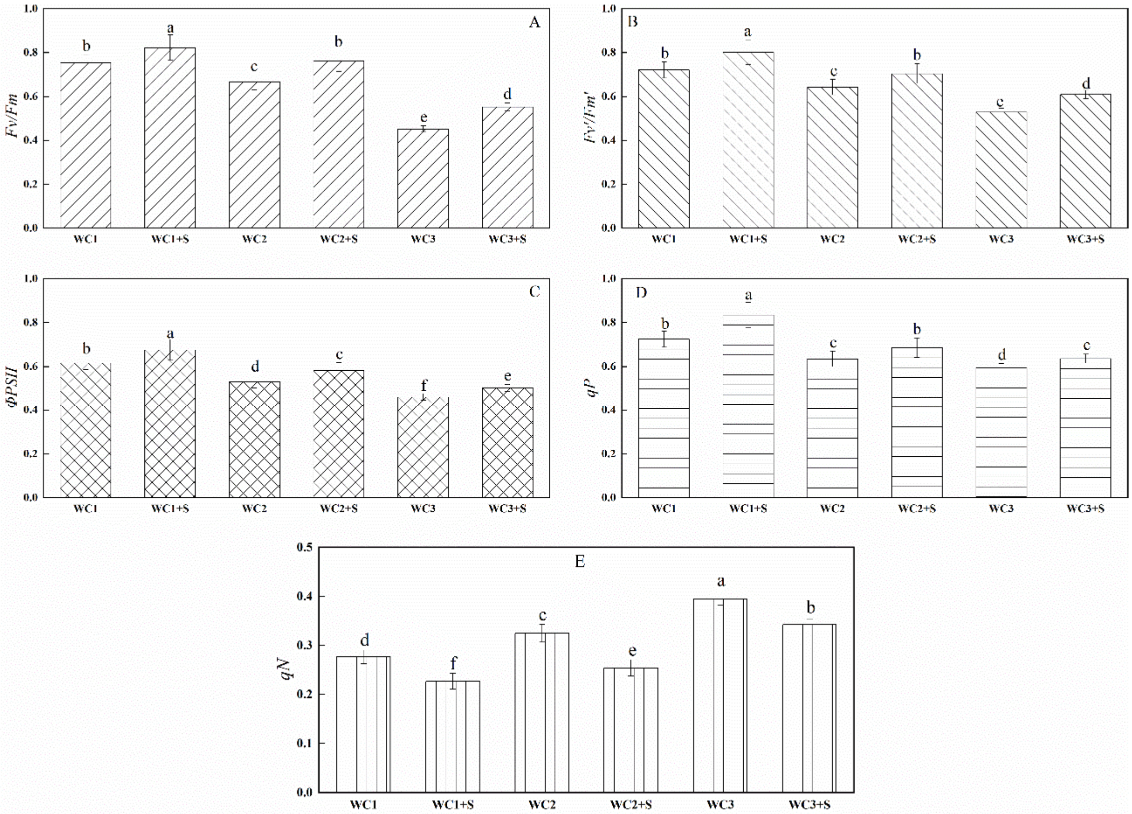

Figure 3. The maximal quantum yield of PSII photochemistry (F_v/F_m) (**A**), the efficiency of excitation capture by the opening of the PSII reaction center (F_v'/F_m') (**B**), the actual PSII efficiency (Φ_{PSII}) (**C**), the photochemical quenching coefficient (qP) (**D**) and the non-photochemical quenching coefficient (qN) (**E**) of *A. canescnes* seedlings under different treatments for 20 days. Values are means ± SE ($n = 18$) and bars indicate SE. In each column, different letters in the same curves indicate significant differences at $p < 0.05$ according to Duncan's test.

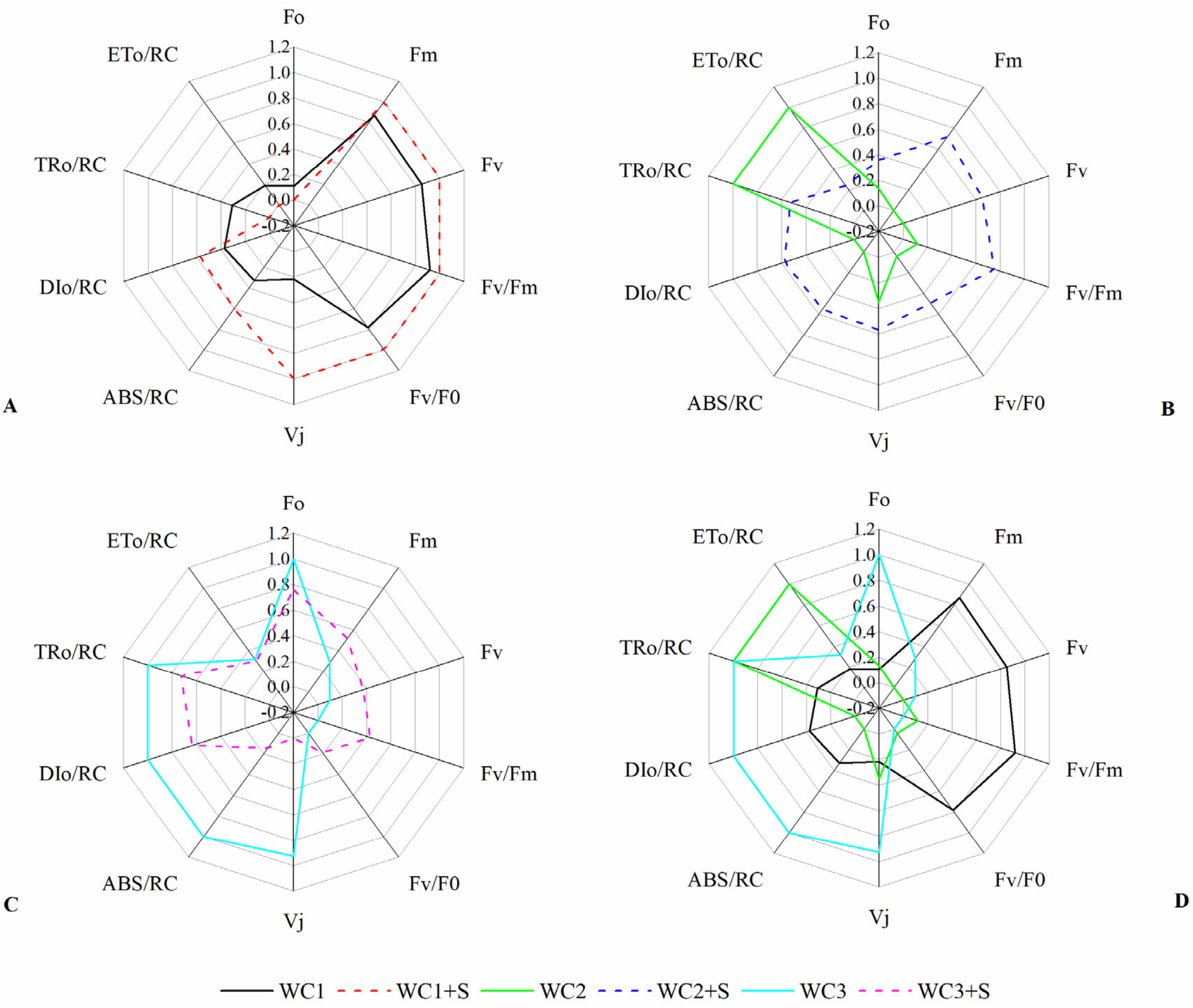

Figure 4. Effects on chlorophyll fluorescence kinetics of *A. canescens* seedlings under different treatments for 20 days. The differences between different groups were shown in (**A**): WC1 and WC1+S, (**B**): WC2 and WC2+S, (**C**): WC3 and WC3+S and (**D**): WC1, WC2 and WC3.

3.4. Leaf Water Status

As shown in Figure 5, the leaf water potential (ψw) significantly decreased with increasing severity of drought stress (Figure 5A). In WC1, WC2 and WC3 treatments, the leaf water potential decreased more than in WC1+S, WC2+S and WC3+S treatments, respectively. Likewise, the leaf ψs decreased gradually with the aggravation of drought stress, and the leaf ψs in WC1+S, WC2+S and WC3+S were always lower than the corresponding treatment in the absence of salt supplementation (Figure 5B). Even though the leaf ψt gradually decreased with the intensification of drought stress, salt supplementation obviously increased ψt compared to the corresponding drought stress group (Figure 5C). The reduction in ψw, ψs and ψt implied that a higher OA capacity could be maintained in *A. canescens* seedlings under drought or salt stress. There was no significant difference in leaf RWC between each drought stress and the corresponding group with salt supplementation except for the WC3 and WC3+S groups (Figure 5D). A significant discrepancy in WC3 and WC3+S was displayed in which the RWC of WC3+S exceeded 6.2% more than that of WC3 (Figure 5D).

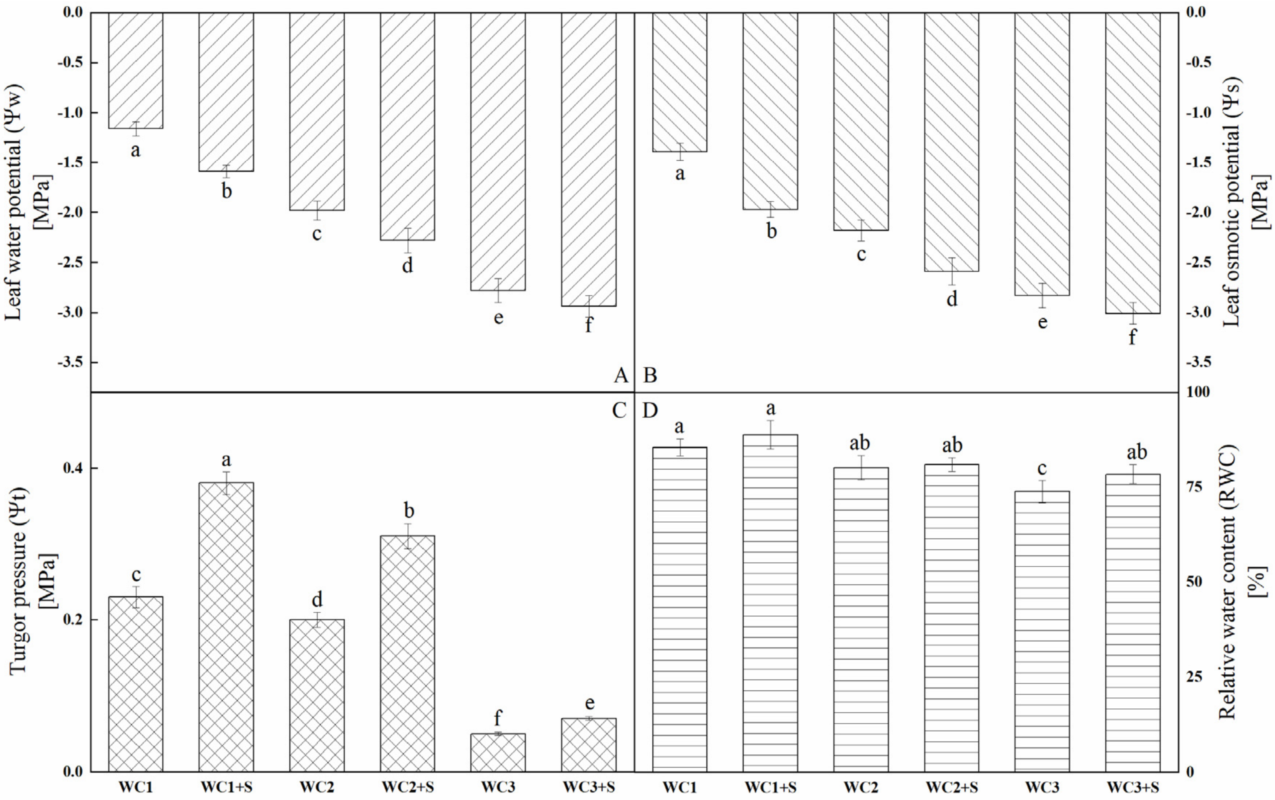

Figure 5. Leaf water potential (ψw) (**A**), leaf osmotic potential (ψs) (**B**), turgor pressure (ψt) (**C**) and relative water content (RWC) (**D**) of *A. canescens* seedlings under different treatments for 20 days. Values are means ± SE (n = 18) and bars indicate SE. In each column, different letters in the same curve indicate significant differences at $p < 0.05$ according to Duncan's test.

3.5. Ion Accumulation and Distribution

Regardless of the salt addition, the increase in the Na^+ concentration in the tissues of *A. canescens* seedlings increased slightly (Figure 6A–C), and the increase in the Na^+ content was obviously higher in the treatment of WC2 and WC3 than WC1, especially in leaves (Figure 6C). An obvious increase in the Na^+ concentration of *A. canescens* seedlings in WC1+S, WC2+S and WC3+S was observed in comparison to the corresponding treatment without salt addition (Figure 6A–C). Drought stress caused an increment in the accumulation of Na^+ in the roots and stems of *A. canescens* either with or without additional salt supplementation, whereas drought stress contributed to a reduction in the accumulation of Na^+ in the leaves of *A. canescens* in the presence or absence of salt solution (Figure 6A–C). It is interesting to note that the increase in the K^+ concentration in root and stem tissues exhibited a sharp decrease under the treatments of drought or salt stress compared to WC1 (normal conditions) (Figure 6D,E), while the increase in the K^+ concentration in leaves remained unchanged in leaves in the treatment either in the presence or absence of salt addition (Figure 6D–F). Additionally, all the tissue K^+ concentrations of *A. canescens* seedlings exposed to drought stress with or without extra salt addition were maintained at a constant level (Figure 6D–F), except for that in WC1 treatment, indicating that the K^+ contents remained relatively stable under both salt supplementation and drought stress.

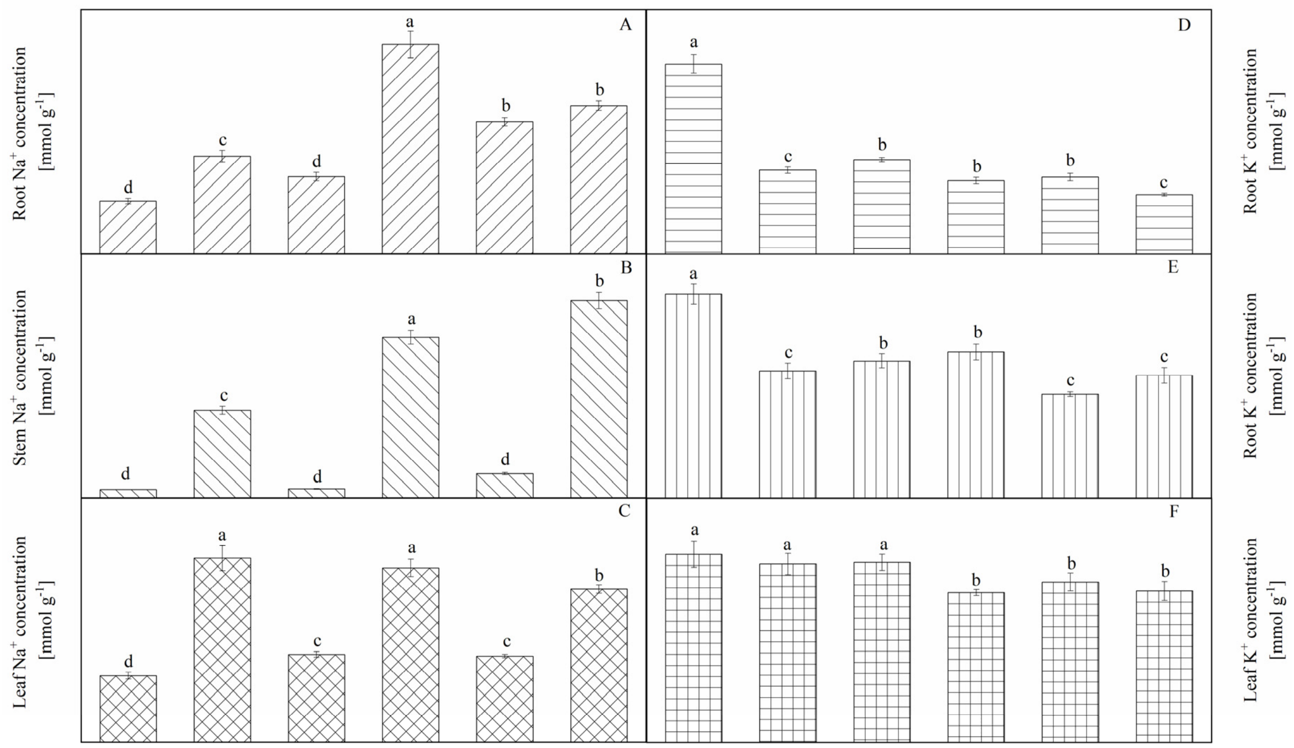

Figure 6. The concentration of Na^+ (**A**–**C**) and K^+ (**D**–**F**) in root, stem and leaf of *A. canescens* seedlings under different treatments for 20 days. Values are means ± SE (n = 18) and bars indicate SE. In each column, different letters in the same curves indicate significant differences at $p < 0.05$ according to Duncan's test.

3.6. Betaine and Free Proline Contents

Compared to WC1, severe drought stress (WC2 and WC3) led to an evident augmentation in free proline and betaine concentrations of *A. canescens* (Figure 7A,B). Furthermore, compared to WC1, WC2 and WC3, the salt-treated groups increased the accumulation of free proline and betaine by at least 5.71 and 1.52%, respectively (Figure 7A,B). The leaf betaine content gradually increased with increasing RWC in the salt-treated plants compared to the water-treated plants, and the leaf betaine content remained almost unaffected under the WC3 and WC3+S treatments (Figure 7B). The leaf-free proline content increased with increasing RWC, and the highest value was obtained under an RWC of 27 ± 2.5%, which was 52.94% higher than that of the WC3 treatment (Figure 7A), while no significant difference was observed between the WC1 and WC1+S treatments. Furthermore, leaf betaine content and free proline content showed the same increasing trend with the increase in RWC of WC1, WC2 and WC3 (Figure 7), implying that appropriate salinity can promote the accumulation of compatible solutes.

3.7. Contributions of the Main Solutes to ψs

When only subjected to drought stress, the contribution of Na^+ to ψs values showed a significant increasing trend by 22.54 and 33.36% in WC2 and WC3 treatments, respectively, compared to the WC1 treatment, whereas a profound decrease was found in the contribution of K^+ to ψs magnitudes by 12.17 and 13.18% in WC2 and WC3 treatments, respectively, compared to the WC1 treatment (Table 3). Moreover, the contribution of leaf betaine to ψs increased by 27.73 and 84.14% in WC2 and WC3 treatments, respectively, compared to the WC1 treatment (Table 3). The contribution of Na^+ to ψs increased by 44.34 and 72.42% in WC2+S and WC3+S treatments, respectively, compared to WC2 and WC3 treatments, and the contribution of K^+ to ψs also increased by 19.28 and 21.92% in WC2+S and WC3+S treatments, respectively, compared to WC2 and WC3 (Table 3). Moreover, the contribution of leaf betaine to ψs increased by 98.61 and 13.10% in the WC2+S and WC3+S treatments in comparison withWC2 and WC3, while the contribution of leaf-free proline to ψs decreased by 41.67 and 30.56% in the WC2+S and WC3+S treatments, respectively, compared to WC2 and WC3 (Table 3).

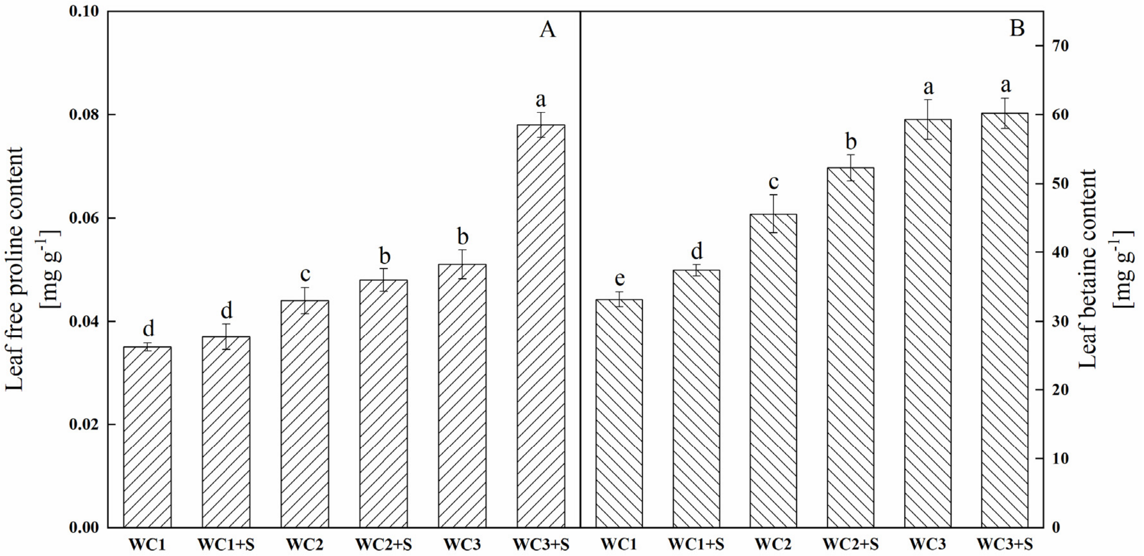

Figure 7. Leaf-free proline (**A**) and betaine (**B**) contents in leaves of *A. canescens* seedlings under different treatments for 20 days. Values are means ± SE (n = 18) and bars indicate SE. In each column, different letters in the same curve indicate significant differences at $p < 0.05$ according to Duncan's test.

Table 3. The contributions of Na^+, K^+, betaine and free proline to leaf osmotic potential (ψs) of *A. canescnes* seedlings grown under different treatments for 20 days. Values are means ± SE (n = 18) and different letters in columns indicate significant differences at $p < 0.05$ (Duncan's multiple range test).

Treatments	Contribution of Na^+ to ψs (%)	Contribution of K^+ to ψs (%)	Contribution of Leaf-Free Proline to ψs (%)	Contribution of Leaf Betaine to ψs (%)
WC1	12.29 ± 0.61 e	70.16 ± 4.84 a	0.38 ± 0.01 a	8.51 ± 0.28 c
WC1+S	17.74 ± 1.21 c	34.39 ± 2.03 d	0.36 ± 0.01 b	5.02 ± 0.11 d
WC2	15.06 ± 0.48 d	61.62 ± 2.71 b	0.22 ± 0.01 d	10.87 ± 0.66 b
WC2+S	23.85 ± 1.17 a	41.02 ± 0.86 c	0.21 ± 0.01 d	9.97 ± 0.36 b
WC3	16.39 ± 0.31 c	60.91 ± 3.41 b	0.15 ± 0.01 e	15.67 ± 0.77 a
WC3+S	21.19 ± 0.59 b	41.93 ± 2.64 c	0.25 ± 0.01 c	11.60 ± 0.42 b

4. Discussion

4.1. Moderate Sodium Salt Facilitates the Growth of A. canescens by Maintaining Good Water Status and Photosynthetic Capacity under Drought Stress

The distribution of ion sodium in the leaves of salt-secreting species is owing to transpiration which is usually divided into two parts, one of which is rapidly secreted by salt glands, and the other part is temporarily stored in the leaves [34]. It has been proposed that some xero-halophytes assimilate abundant sodium ions from sterile soil and stock them, which can result in stimulation of plant growth, especially when exposed to the severe environment of drought or saline soil [7,19]. In the present study, compared to the corresponding drought stress treatments (WC1, WC2 and WC3), the additional salt supplement (WC1+S, WC2+S and WC3+S) significantly increased the plant growth parameters, including plant height, ground diameter, dry mass, fresh mass and RGR, of *A. canescens* seedlings (Table 2). Furthermore, the Na^+ distribution in tissues of *A. canescens* in the presence of salt supplementation implied that moderate salt could facilitate *A. canescens* acclimatize to drought stress through accumulating a large amount of Na^+ in plants (Figure 6A–C), and concomitantly, the augmentation of leaf RWC (Figure 5D), P_n, g_S and T_r (Figure 1A–C) also contributed to the stimulation of plant growth. These results indicated that a certain concentration of salt supplement could help *A. canescens* maintain good water status and photosynthesis under drought stress which led to a good growth performance. Similar results have been found in some halophytes [1,35,36].

Photosynthesis is a necessary process for plants to retain growth and is strongly affected by stomatal limitations [19,37]. The P_n, g_S and T_r decreased with increasing severity of drought stress in the present study. A reasonable explanation for this phenomenon is that the inactivation of photosynthetic cells leads to nonstomatal limitations in plants under severe drought stress [38]. However, the additional salt supplement markedly alleviated the suppressive impacts of leaf ψs on the photosynthesis of *A. canescens* under the same withholding water content (Figure 1A–C and Figure 5A,B). The results indicated that moderate concentrations of sodium salt could enhance the capability of *A. canescens* to adapt to drought conditions, especially under severe conditions; meanwhile, an obvious increase in ψt was found in the presence of additional salt supplementation, which suggested that a moderate concentration of sodium salt might enhance the g_S via the aggrandizement of ψt and then result in the enhancement of P_n. This finding coincides with our results that tissue ψs had a great influence on cell turgor, which depends on the extent of stomatal opening [39]. According to Hedrich and Tahjib-UI-Arif, the balanced water status and accumulated biomass in plants are closely dependent on transpiration and stomata [40,41]. The increasing trend of P_n, g_S and T_r and the relatively constant level of WUE (Figure 1) also demonstrated that transpiration and stomatal opening degree improved the water status and photosynthetic competence by accelerating the water transport and carbon assimilation [42].

Overall, a great amount of sodium ion accumulated in the plant could consequently enhance the water status and photosynthetic capability, and thus improve the growth of *A. canescens*. Therefore, we believe that moderate sodium salt accelerates the growth of *A. canescens* under drought stress.

4.2. Moderate Sodium Salt Improves the Adaptability of A. canescens to Drought Stress by Mitigating the Suppression of PSII

Chlorophyll fluorescence analysis has been applied as another effective factor to detect and determine the effects on plant growth in a stressful environment [43]. In the present study, although an obvious O-J-I-P curve was found in each treatment, drought stress still had the greatest impact on chlorophyll fluorescence. The most conspicuous decrease was found at points J and I, which implied that severe drought could result in the reduction in the absorption of chloroplasts in light energy and PSII activity [44]. In contrast, the corresponding treatment with additional salt supplementation (WC1+S, WC2+S and WC3+S) had higher chlorophyll fluorescence values at steps J and I, which indicated that moderate salt supplementation could relieve the mild inhibitory of drought on the absorption capacity of chloroplasts. In the present study, the chlorophyll fluorescence at points J and I in WC1, WC2 and WC3 treatments were markedly more increased than WC1+S, WC2+S and WC3+S (Figure 2). This may be ascribed to the reduction in primary quinone acceptor (QA) resulting in excessive QA^- accumulation in the cell [33]. Moreover, the chlorophyll fluorescence at points J and I were lower with the aggradation of drought stress, which may be because the reduction in QA and block of plastoquinone during the electron transfer process led to the decrease in QA^-. This result is in accordance with our previous study of *Lycium ruthenicum* Murr [45].

The decline in F_v/F_m implied that the photochemical efficiency of PSII was decreased and the photosynthetic apparatus was impaired which is attributed to the stress environment [46]. In general, the values of F_v/F_m are equal to $0.75 \leq F_v/F_m \leq 0.86$ which means F_v/F_m is relatively constant for different plants exposed to a normal environment and the photosynthetic organ is in good condition [47]. In other words, a value of F_v/F_m lower than 0.75 means that the plants have been under stress conditions and have suffered from damage. As our results showed, even though the F_v/F_m under severe drought stress was lower than 0.75 in all the treatments, the F_v/F_m ratio in WC1, WC2 and WC3 treatments was lower than WC1+S, WC2+S and WC3+S treatments, which indicated that a certain concentration of sodium salt could alleviate the light suppression of drought stress. The increments in the F_v/F_m ratio could also imply that the photosynthetic conversion efficiency of PSII was stimulated [48,49]. F_v'/F_m' can indicate the ability to absorb sunlight and reflect the actual captured energy transfer efficiency of the photosynthetic RC when it is partially closed [49]. In the present study, the values of F_v'/F_m' decreased with increasing severity of drought stress. This result indicated that most of the light energy was not photochemically quenched under drought stress.

The actual Φ_{PSII} decreased more with the more severe drought stress, while the addition of salt improved Φ_{PSII} compared to the corresponding drought stress groups (WC1, WC2 and WC3). The main reason for this phenomenon may be due to the reduction in *qP*. *qP* reflects the efficiency of light conversion and the state of QA^-, which can result in the reduction in Φ_{PSII}. *qN* reflects the portion of excessive light energy that was absorbed from the antenna pigment by the PSII RC and then dissipated in the form of heat energy. *qN* can indicate the extent of damage to the photosynthetic mechanism. Short-term stress can increase *qN* to reduce non-photosynthetic energy and increase the ability to protect photosynthetic apparatus from damage. Therefore, non-photochemical quenching has a certain protective effect on photosynthetic apparatus. In the present study, the seedlings under drought stress had lower Φ_{PSII} and *q*P, while those with salt supplement seedlings had higher Φ_{PSII} and *q*P compared to the corresponding group without salt supplement. Furthermore, *q*N exhibited a contrasting trend compared to Φ_{PSII} and *q*P. These results demonstrated that mild stress had a positive effect on electron transport in the PSII RC of *A. canescens*, and the absorbed light energy gradually dissipated as heat resulting in the closure of RC to protect itself. This phenomenon reported in the literature is in line with our result [45].

The increase in ABS/RC and DIo/RC was significant under drought conditions, which could perform a decrease in the conversion efficiency of light energy leading to a self-protective photosynthesis mechanism, which can absorb more light energy and use it for RC activities, thus alleviating the damage caused by stress conditions. This result is in accordance with our previous study of *Lycium ruthenicum* Murr [45]. As shown in Figure 4, TRo/RC, ETo/RC and Vj increased with the severity of drought stress in all the treatments, which indicated that the photochemical function may be damaged as a consequence of the destruction of the PSII RC [50]. However, the salt supplement group (WC1+S, WC2+S and WC3+S) had lower values of TRo/RC, ETo/RC and Vj than the group exposed to drought stress without extra salt addition (WC1, WC2 and WC3). This result demonstrated that mild salt supplementation could help the PSII RC avoid stress-induced damage. Hence, the presence of Na^+ is beneficial to photophosphorylation and electron transport in the PSI and PSII systems.

4.3. Moderate Sodium Salt Promotes the Drought Resistance of A. canescens by Improving the Function of Compatible Solutes in OA

Maintaining a stable intracellular balance of ions is an indispensable pathway in physiological processes, and becomes a more critical factor for plants to survive in arid environments [51]. Numerous studies have discussed sodium nutrition in the *Atriplex* genus, while they only consider saline conditions [3]. It was proposed that the accumulation and sequestration of sodium ions in vacuoles could help plants enhance the OA process and thus alleviate the light suppression of stress [1,52]. In this study, an additional sodium salt supplement conspicuously promoted the Na^+ concentration in *A. canescens* seedlings (Figure 6A–C). Moreover, K^+ is also one of the necessary elements for plants, and it is important in physiological and biochemical processes such as OA, maintenance of cell balance and enzyme activation [53]. In addition, Na^+ could substitute K^+ to some extent in

OA [54,55]. As shown in Figure 6, the leaf Na^+ absorption was increased, whereas no significant changes were observed in leaf K^+ concentration. This implied that *A. canescens* selected more Na^+ than K^+ to improve growth under drought stress, which showed that *A. canescens* has the same properties as the halophytes *Salvadora persica* and *Suaeda salsa* [56,57].

Drought stress can often result in producing excessive reactive oxygen species (ROS) in plants, which leads to lipid peroxidation and further destroy membranes. Proline and betaine act as osmotic protectants and free radical scavengers to attract enough water in plants to sustain ψt [58]. When seedlings are subjected to stress, the organic OA substances accumulated in plants can improve the water retention capacity of plants, prevent cell dehydration and stabilize cell structure; on the other hand, they can provide necessary nutrients for cells [59,60]. When *A. canescens* is subjected to abiotic stress, the proline and betaine content increases rapidly, and the RWC and the ψs of the cells are maintained by OA, thereby improving the resistance of the plants. In this study, the contents of proline and betaine increased under different treatments, and the ψs adjustment substance maintained a higher capability of OA when subjected to mild and moderate stress (Figure 7). Similar phenotypes were also reported in Pan's research [27]. As is well known, excessive inorganic ions or compatible solutes could cause higher OA in plants under salt stress. Thus, the contributions of solutes to ψs were evaluated under all the treatments. The concentration of K^+ to OA was significantly decreased in the presence of 150 mM sodium salt, while the contribution of Na^+ in mesophyll cells of *A. canescens* can contribute to OA to deal with abiotic stress (Table 3). In the present study, the contribution of leaf-free proline to OA and the contribution of leaf betaine to OA both decreased in the presence of additional sodium salt (Table 3). These results showed that an appropriate concentration of sodium salt could stimulate the capability of *A. canescens* to adapt to abiotic stress.

Plants usually suffer from severe water deficits from drought stress ascribed to leaves exposed to drought conditions and strong transpiration. The water status is dominated by cell ψt which can lead to water deficit and change the shapes, arrangements and spatial distribution of cells in plant tissues. In the present study, drought stress caused an obvious decline in ψt and RWC, while mild sodium salt increased these two parameters in comparison with the corresponding treatments (Figure 5C,D). Thus, we can conclude that moderate sodium salt could relieve the impact of severe drought stress on *A. canescens* by improving ψt, which is in line with the previous report by He, et al. [1]. Numerous studies have shown that the water absorption and utilization ability of plans could be enhanced by decreasing leaf ψs [10,14]. The results in the present study showed that ψs markedly decreased with more severe drought stress and that the rate of decrease was more rapid with proper salt supplementation (Figure 5B). This result suggested that moderate sodium salt could enhance the capability of *A. canescens* to acclimatize to drought stress by improving the function of compatible solutes in OA.

5. Conclusions

In this paper, we evaluated the water status, photosynthetic and biochemical parameters, and ion dynamics of *A. canescens* under drought stress with or without extra sodium salt addition (150 mM). The results demonstrate that moderate sodium salt supplementation has a positive impact on the plants to alleviate the deleterious influence of drought stress. The growth of plants in the presence of mild salt supplementation can be promoted via the accumulation of substantial sodium ion and betaine in leaves participating in OA to sustain relatively a high ψt and RWC in leaves while reducing the leaf ψs. Therefore, the photosynthetic capacity is enhanced and light suppression of drought stress on PSII is relieved to contribute to seedlings growth and resistance to drought stress. These findings laid a basis and reference for *A. canescens* to be cultivated under drought stress and its physiological mechanisms reacting to harsh environments.

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Abbreviations

OA	Osmotic adjustment
SRWC	Soil relative water content
FW	Fresh weight
DW	Dry weight
TW	Turgid weight
RGR	Relative growth rate
PAR	Photosynthetically active radiation
RWC	Relative water content
P_N	Net photosynthetic rate
g_S	Stomatal conductance
T_r	Transpiration rate
WUE	Water use efficiency
PSII	Photosystem II
RC	Reaction center
F_o	Initial fluorescence
F_m	Maximal fluorescence
F_v	Variable Fluorescence
$F_\mathrm{v}/F_\mathrm{m}$	Maximal quantum yield of PSII photochemistry
Φ_PSII	Actual PSII efficiency
qP	Photochemical quenching coefficient
qN	Nonphotochemical quenching coefficient
F_v/F_0	Potential efficiency of PSII photochemistry
$\mathrm{V_j}$	Relative variable fluorescence at the J step
ABS/RC	Light absorption energy flux per RC
DIo/RC	Relative energy flux per PSII RC
TRo/RC	Trapped energy flux per RC
ETo/RC	Maximum electron transport flux per PSII RC
ψw	Leaf water potential
ψs	Leaf water osmotic potential
ψt	Leaf turgor potential
COP	Calculated osmotic potential
CR	Contribution rate to the leaf ψs

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