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Effect of salt stress on the growth and photosystem II photochemical characteristics of *Lycium ruthenicum* Murr. seedlings

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Abstract

The present study aimed to determine effects of salt stress on *Lycium ruthenicum* Murr. seedlings. Our results showed that mild and moderate salt stress were beneficial to *L. ruthenicum* seedling growth. Minimal fluorescence increased and maximum fluorescence decreased gradually with the increasing levels of salt stress. Absorption flux per reaction center (RC), trapped energy flux per RC, and trapped energy flux per optical cross section (CS) increased significantly, while electron transport flux per CS decreased with salt stress duration and rising salt concentration. During salt stress, there was a gradual decline in probability that a trapped exciton moves an electron into the trapped electron transport chain beyond Q_A, quantum yield for electron transport, and performance index on absorption basis. However, gradual increases in relative variable fluorescence, dissipated energy flux per RC, and dissipated energy flux per CS were found in response to salt stress.

Additional key words: chlorophyll fluorescence kinetics; OJIP transient; photosynthesis; salt tolerance.

Introduction

During their life time, plants may face various abiotic stresses, such as salt excess, drought, and temperature fluctuations, all of which may negatively affect their full growth potential (Forni *et al*. 2017, Yousuf *et al*. 2017, George *et al*. 2018). Salt stress is the most serious abiotic stress that threatens agricultural sustainability by negative impact on plant growth and crop production (Bray *et al*. 2000, Azeem *et al*. 2017, Yousuf *et al*. 2017). The accumulation of salts in soil leads to water stress and nutrient deficiency in plants (Arshi *et al*. 2012). Salt stress may lead to redox imbalances, ion toxicity, oxidative damage, and water deficit by destroying ion and osmotic homeostasis, which can lead to the inhibition of photosynthesis, metabolic dysfunction, and damage to cellular structures within plant cells (Wei *et al*. 2017). Salt stress can affect light reaction, such as chlorophyll photoenergy conversion and electron transport, and dark reaction in plants (Sudhir and Murthy 2004, Zhang *et al*. 2009, Ashraf and Harris 2013, Zhang *et al*. 2013, Zhou *et al*. 2016). Therefore, the response and adaptation of plant growth, biomass allocation, and chlorophyll characteristics to salt stress is crucial in further discussing plant adaptation to salt.

Lycium ruthenicum Murr., which belongs to *Solanaceae* family, is a perennial deciduous shrub tolerant to drought and salt. This plant, which is mainly distributed in Northwest China, is important in ecology, medicine, forestry, and particularly in water and soil conservation. Rich in protein and polysaccharides, the *L. ruthenicum* fruit has been recorded in Tibetan medical classic 'Jing Zhu Ben Cao' as a traditional herb (Zheng *et al*. 2011) and has become increasingly expensive due to the acceptance of its medicinal value. Owing to a serious damage to natural vegetation, *L. ruthenicum* grew fewer in number, and the species was listed as an important conservation plant. Thus, effective management and protection of

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Abbreviations: ABS/CS_0 – absorption flux per CS; ABS/RC – absorption flux per RC; CK – control; CS – optical cross-section; DAE – days of experiment; DI_0/CS_0 – dissipated energy flux per CS; DI_0/RC – dissipated energy flux per RC; ET_0/CS_0 – electron transport flux per CS; ET_0/RC – electron transport flux per RC; F_0 – minimal fluorescence; F_m – maximum fluorescence; F_v/F_m – maximum quantum yield of PSII; OJIP – fast chlorophyll fluorescence transients; PI_{abs} – performance index on absorption basis; RC – reaction center; RC/CS_0 – amount of active PSII RC per CS; ST1 – 0.1 mol(salt) L^{-1}; ST2 – 0.3 mol(salt) L^{-1}; ST3 – 0.5 mol(salt) L^{-1}; R:S – the root to shoot ratio; TR_0/CS_0 – trapped energy flux per CS; TR_0/RC – trapped energy flux per RC; V_j – relative variable fluorescence; φ_{DO} – quantum yield at t = 0 for energy dissipation; φ_{EO} – quantum yield for electron transport; φ_{PO} – maximum quantum yield of primary photochemistry; ψ_o – probability that a trapped exciton moves an electron into the trapped electron transport chain beyond Q_A.
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L. ruthenicum should be developed. Field investigation results indicated a reduced seedling number; whether salt stress affects a seedling number required further research. Several studies suggested that seed germination was affected by drought and salt (He *et al*. 2011, Han *et al*. 2014). However, information on seedling adaptive capacity and mechanism of plant adaptation under salt environments is still lacking.

Thus, the present study aimed to determine the effect of salt stress on the biomass allocation and chlorophyll (Chl) fluorescence of *L. ruthenicum* seedlings. Comparison of these responses benefits the determination of salt tolerance capacity and mechanism in *L. ruthenicum* cultivars and provides theoretical basis for the vegetation restoration of *L. ruthenicum*.

Materials and methods

Plant material and salt stress: The study site was located in Hexi University Practice Base of Agriculture, Zhangye City (37°28'N, 97°20'E) in Gansu Province, China. The climate was a continental environment with an annual average temperature, sunshine duration, rainfall, and evaporation of 6°C; 3,106 h; 113–120 mm; and 2,291 mm, respectively. Seeds were harvested in August 2015 at Ganzhou District, Gansu Province, China. After washing, seeds were dried for one week under direct sunlight and then stored at 4°C prior to experiments. After the seeds were surface-sterilized with 2% potassium permanganate solution, five seeds were sowed in each pot (23 cm in diameter and 20 cm in height) on 15 March, 2016, with the pots containing the same amount of soil, sandy soil, and humus (1:2:1). When the seedling formed 2–3 leaves, three seedlings were retained in each pot. Stress treatment was initiated on 10 May, 2017. The experiment consisted of control and salt-treated groups, with ten pots assigned to each group. The control and stressed groups were subjected to normal watering. After experiment, the stress treatment was applied to three groups. The salt-treated group was watered once a week, and 0.1 mol L^{-1} (ST1), 0.3 mol L^{-1} (ST2), and 0.5 mol L^{-1} (ST3) NaCl salt solutions were used. At days 0, 7, 14, and 21 (DAE), growth parameters, biomass, and fluorescence parameters were measured in control and stress-treated plants.

Growth parameters: At 0, 7, 14, and 21 DAE, height, base diameter, branching number, and root length were measured in control and stressed plants. Plant height and root length were measured using a tape. The seedlings were harvested, divided into roots, stems, and leaves, and dried in an oven for 48 h at 70°C for biomass determination. The total biomass was the sum of root, stem, and leaf dry mass. Root:shoot (R:S) ratio was calculated as the root dry mass (DM) divided by the aboveground DM.

Fast Chl fluorescence induction curve: The fluorescence parameters were determined on the attached leaf by a plant efficiency analyzer (*Handy-PEA*, *Hansatech Instrument Ltd*., UK) with an actinic light of 3,000 μmol(photon) m^{-2} s^{-1} using the procedure described by Strasser *et al*. (1995). The selected leaves of control and stressed plants were placed in darkness for 20 min before the fluorescence parameters were measured at 0, 7, 14, and 21 DAE. On the basis of the theory of energy fluxes in PSII, we obtained several fluorescence parameters from the OJIP transient curve *via* the following original values of fluorescence intensity at 50 μs (F_0) and the maximum fluorescence intensity (F_m). Several parameters selected to quantify the PSII behavior of *L. ruthenicum* Murr. were calculated from the above original data (Strasser *et al*. 1995).

Statistical analysis was performed using *SPSS18.0* statistical software package for *Windows*. All data were subjected to one-way analysis of variance (*ANOVA*). LSD multiple comparison tests were used to separate significant differences between all treatments at 0.05 level. Standard error (SE) was calculated, as shown in figures and tables.

Results

Growth: In all treatments, height and base diameter were significantly higher in ST1 than those in other treatments (Fig. 1*A*,*B*). With increasing stress duration, the height, base diameter, branching number, and crown increased in all treatments. However, ST1 and ST2 presented higher growth parameters compared to other treatments. In CK, ST1, ST2, and ST3, height increased by 3.0, 9.9, 4.9, and 2.7% at 7 DAE compared with 0 DAE, respectively. At 21 DAE, height increased by 15.2, 34.9, 21.0, and 11.0% compared to those of 0 DAE, while the base diameter increased by 88.6, 167.6, 100.5, and 56.2% compared to those at 0 DAE in CK, ST1, ST2, and ST3 treatments, respectively. The branching number increased by 12.9, 40.0, 15.6, and 12.5%, and the crown increased by 41.4, 83.5, 61.7, and 35.5% at 21 DAE compared to that at 0 DAE in CK, ST1, ST2, and ST3, respectively (Fig. 1*C*,*D*).

Biomass: The dry mass allocation of stress-treated seedlings was significantly different from that of the control treatment (Table 1). With increasing treatment duration, the total DM, leaf mass, stem mass, and root mass of seedlings increased across all treatments as follows: ST1 > ST2 > CK > ST3. At 21 DAE, the total DM of ST1 seedling increased by 29.6, 22.6, and 47.4% compared to those in CK, ST2, and ST3, respectively. The R:S ratios in ST1 and ST2 were higher at 21 DAE compared to those in other treatments, but those in CK and ST3 were higher at 14 DAE. Root length increased with treatment duration in all treatments. However, at the same treatment time, the root length exhibited the following relation for different treatments: ST1 > ST2 > CK > ST3 at 14 and 21 DAE. At 21 DAE, root length of CK, ST1, ST2, and ST3 seedling increased by 62.1, 119.1, 68.1, and 46.2% compared to those at 0 DAE

Chl fluorescence transients: After *L. ruthenicum* seedling leaves were exposed to pulse light intensity of saturation, the Chl fluorescence value increased rapidly through dark adaptation. However, the value eventually decreased (Fig. 2). The OJIP curves showed little change at different

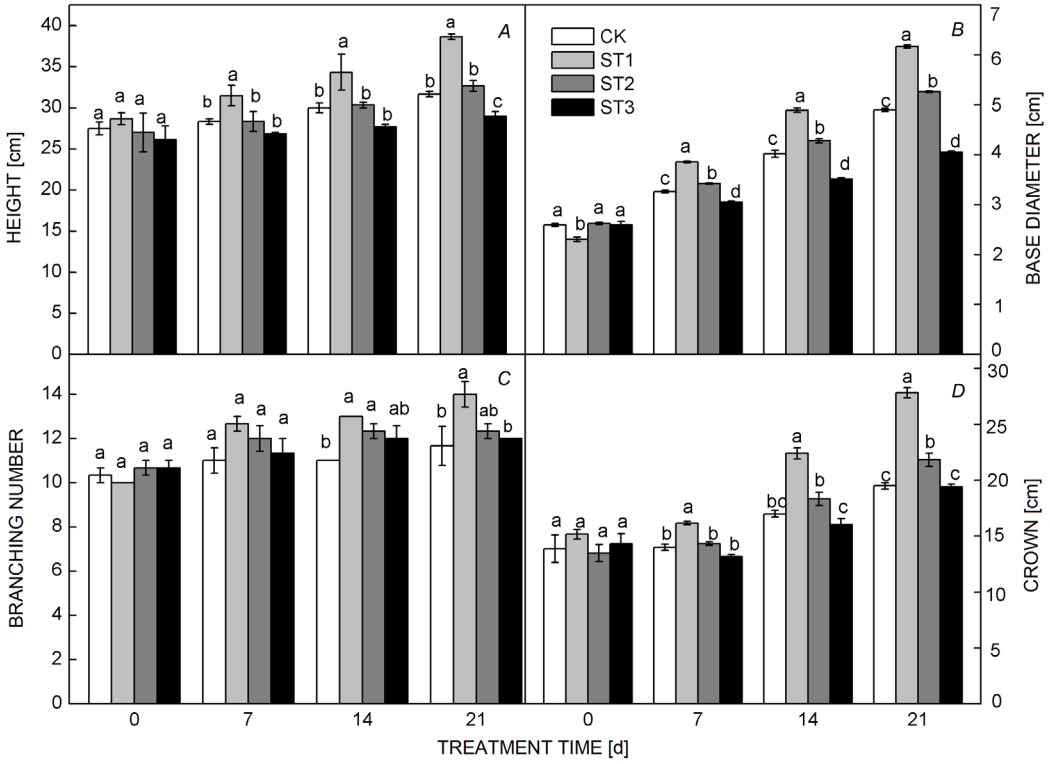

Fig. 1. Seedling height (*A*), base diameter (*B*), branch number (*C*), and crown (*D*) of control and salt-treated *Lycium ruthenicum* Murr. seedlings. Data are means ± SE ($n = 5$). *Different letters* indicate significant differences between treatments at $P<0.05$. CK – control; salt treatments: ST1 – 0.1 mol L^{-1}, ST2 – 0.3 mol L^{-1}, ST 3 – 0.5 mol L^{-1}.

Table 1. Seedling biomass, root mass, root to shoot ratio (R:S), and root length of control and salt-treated *Lycium ruthenicum* Murr. seedlings. Data are means ± SE ($n = 5$). *Different letters* indicate significant differences between treatments at $P<0.05$. CK – control, DAE – days of experiment, DM – dry mass, salt treatments: ST1 – 0.1 mol L^{-1}, ST2 – 0.3 mol L^{-1}, ST 3 – 0.5 mol L^{-1}.

Treatment	DAE	Total DM [g]	Leaf DM [g]	Stem DM [g]	Root DM [g]	R:S	Root length [cm]
CK	0	1.29 ± 0.02^{a}	0.74 ± 0.01^{a}	0.34 ± 0.01^{a}	0.21 ± 0.01^{a}	0.20 ± 0.01^{a}	14.50 ± 0.29^{a}
	7	1.63 ± 0.01^{b}	0.84 ± 0.00^{b}	0.47 ± 0.00^{b}	0.32 ± 0.00^{b}	0.25 ± 0.00^{b}	17.50 ± 0.29^{b}
	14	2.16 ± 0.04^{c}	1.12 ± 0.03^{c}	0.61 ± 0.00^{c}	0.44 ± 0.01^{c}	0.26 ± 0.01^{c}	20.50 ± 0.29^{c}
	21	3.07 ± 0.01^{d}	1.73 ± 0.01^{d}	0.82 ± 0.00^{d}	0.52 ± 0.00^{d}	0.20 ± 0.00^{a}	23.50 ± 0.29^{d}
ST1	0	1.32 ± 0.01^{a}	0.73 ± 0.01^{a}	0.34 ± 0.00^{a}	0.24 ± 0.01^{a}	0.22 ± 0.00^{a}	14.83 ± 0.44^{a}
	7	2.02 ± 0.01^{b}	0.96 ± 0.00^{b}	0.55 ± 0.01^{b}	0.50 ± 0.00^{b}	0.33 ± 0.00^{b}	18.33 ± 0.33^{b}
	14	2.97 ± 0.01^{c}	1.48 ± 0.01^{c}	0.90 ± 0.00^{c}	0.59 ± 0.01^{c}	0.25 ± 0.00^{c}	22.50 ± 0.29^{c}
	21	3.98 ± 0.01^{d}	2.09 ± 0.02^{d}	1.23 ± 0.01^{d}	0.66 ± 0.01^{d}	0.20 ± 0.00^{d}	32.50 ± 0.29^{d}
ST2	0	1.30 ± 0.01^{a}	0.72 ± 0.01^{a}	0.35 ± 0.01^{a}	0.23 ± 0.01^{a}	0.22 ± 0.01^{a}	15.17 ± 0.60^{a}
	7	1.84 ± 0.01^{b}	0.88 ± 0.01^{b}	0.54 ± 0.01^{b}	0.42 ± 0.00^{b}	0.29 ± 0.00^{b}	20.00 ± 0.58^{b}
	14	2.56 ± 0.01^{c}	1.32 ± 0.01^{c}	0.76 ± 0.01^{c}	0.49 ± 0.00^{c}	0.23 ± 0.00^{c}	21.83 ± 0.44^{c}
	21	3.25 ± 0.06^{d}	1.77 ± 0.05^{d}	0.94 ± 0.00^{d}	0.54 ± 0.00^{d}	0.20 ± 0.00^{d}	25.50 ± 0.29^{d}
ST3	0	1.29 ± 0.01^{a}	0.74 ± 0.00^{a}	0.34 ± 0.00^{a}	0.22 ± 0.00^{a}	0.20 ± 0.00^{a}	15.50 ± 0.29^{a}
	7	1.52 ± 0.01^{b}	0.86 ± 0.02^{b}	0.36 ± 0.01^{b}	0.31 ± 0.01^{b}	0.25 ± 0.01^{b}	16.83 ± 0.44^{b}
	14	1.83 ± 0.01^{c}	0.91 ± 0.01^{b}	0.54 ± 0.00^{c}	0.37 ± 0.00^{c}	0.26 ± 0.00^{ab}	19.50 ± 0.29^{c}
	21	2.70 ± 0.04^{d}	1.56 ± 0.04^{c}	0.72 ± 0.01^{d}	0.42 ± 0.00^{d}	0.19 ± 0.00^{c}	22.67 ± 0.33^{d}

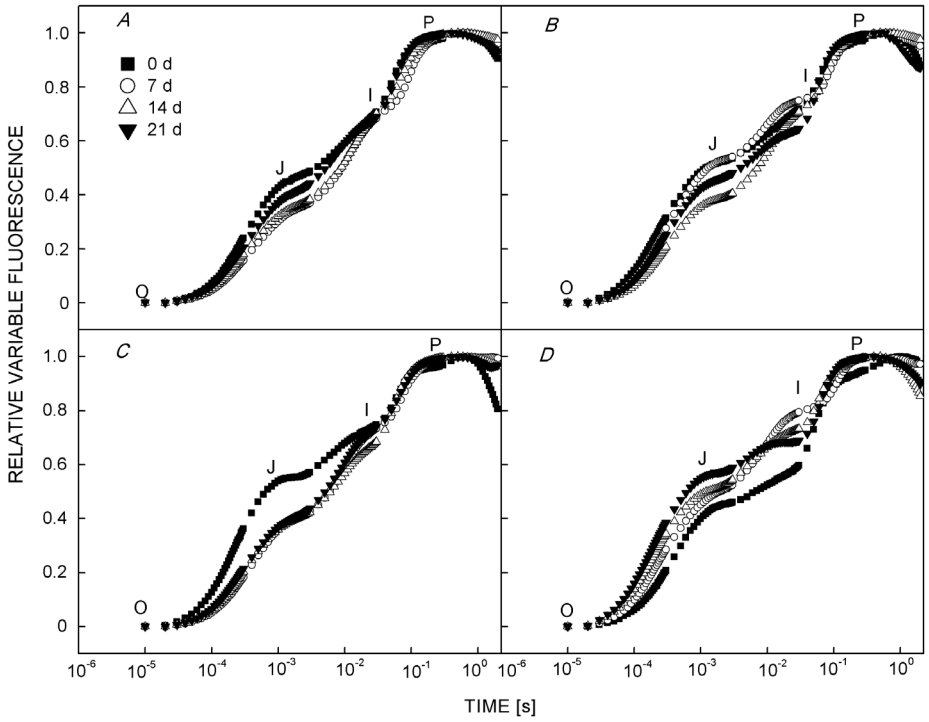

Fig. 2. Fast chlorophyll fluorescence transients (OJIP) of control (CK) (*A*), and salt-treated: 0.1 mol L^{-1} (ST1) (*B*), 0.3 mol L^{-1} (ST2) (*C*), and 0.5 mol L^{-1} (ST3) (*D*) *Lycium ruthenicum* Murr. seedlings.

Table 2. Changes of the minimal fluorescence (F_0), maximum fluorescence (F_m), maximum quantum yield of PSII (F_v/F_m), and relative variable fluorescence (V_j) of *Lycium ruthenicum* Murr. seedlings under control (CK), and salt treatments: 0.1 mol L^{-1} (ST1), 0.3 mol L^{-1} (ST2), and 0.5 mol L^{-1} (ST3). Data are means ± SE (n = 5). *Different letters* indicate significant differences between treatments at P<0.05. DAE – days of experiment.

Treatment	DAE	F_0	F_m	F_v/F_m	V_j
CK	0	192.33 ± 3.48^a	1455.67 ± 4.91^a	0.84 ± 0.00^a	0.39 ± 0.05^a
	7	193.80 ± 6.31^a	1422.80 ± 22.18^a	0.84 ± 0.01^a	0.36 ± 0.04^a
	14	193.40 ± 14.46^a	1392.80 ± 23.81^a	0.81 ± 0.01^b	0.37 ± 0.01^a
	21	199.40 ± 2.69^a	1422.80 ± 24.37^a	0.81 ± 0.01^b	0.39 ± 0.04^a
ST1	0	190.33 ± 1.33^a	1434.67 ± 4.81^a	0.83 ± 0.01^a	0.37 ± 0.01^a
	7	216.40 ± 14.23^a	1327.60 ± 37.20^b	0.82 ± 0.00^a	0.40 ± 0.06^a
	14	254.80 ± 11.91^b	1060.20 ± 9.35^c	0.81 ± 0.01^a	0.42 ± 0.02^a
	21	275.40 ± 2.82^b	1028.80 ± 38.07^c	0.77 ± 0.02^b	0.43 ± 0.01^a
ST2	0	191.33 ± 2.85^a	1462.00 ± 12.86^a	0.84 ± 0.00^a	0.35 ± 0.01^a
	7	219.20 ± 5.08^a	1325.00 ± 19.90^b	0.81 ± 0.00^a	0.43 ± 0.01^b
	14	266.20 ± 15.09^b	1040.40 ± 10.73^c	0.78 ± 0.03^a	0.44 ± 0.01^{ab}
	21	292.20 ± 15.23^b	1011.60 ± 23.64^c	0.70 ± 0.01^b	0.45 ± 0.01^b
ST3	0	190.00 ± 2.89^a	1459.33 ± 15.25^a	0.83 ± 0.01^a	0.39 ± 0.04^a
	7	260.60 ± 15.19^b	1300.00 ± 58.78^a	0.80 ± 0.00^a	0.51 ± 0.03^b
	14	320.20 ± 10.38^c	1037.00 ± 48.89^b	0.68 ± 0.02^b	0.55 ± 0.02^b
	21	369.80 ± 21.40^d	991.20 ± 75.78^b	0.63 ± 0.05^b	0.59 ± 0.04^b

stages under CK treatment. Under salt stress, the initial fluorescence O step did not change compared to that in CK. The O–J, J–I, and I–P stages clearly increased under salt stress treatment compared with that under CK treatment. However, the highest values of J and I appeared at 21 and 7 DAE in ST3.

Chl fluorescence transient parameters: F_0 remained

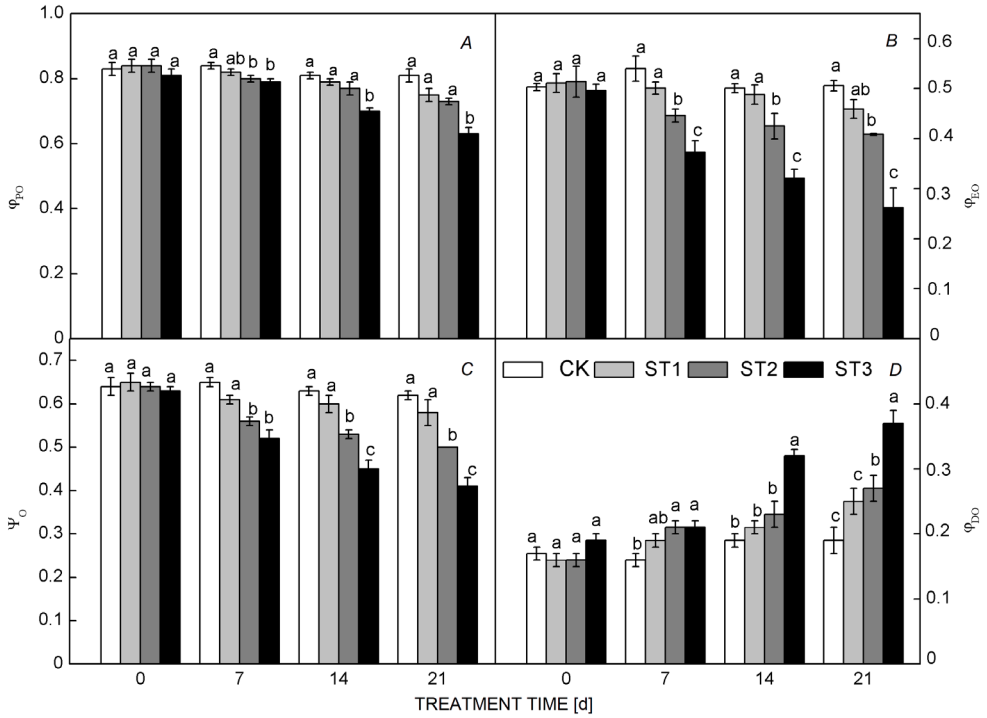

Fig. 3. Maximum quantum yield of primary photochemistry (φ_{PO}) (*A*), quantum yield for electron transport (φ_{EO}) (*B*), probability that a trapped exciton moves an electron into the trapped electron transport chain beyond Q_A (ψ_o) (*C*), and quantum yield at t = 0 for energy dissipation (φ_{DO}) (*D*) of control and salt-treated *Lycium ruthenicum* Murr. seedlings. Data are means ± SE (n = 5). *Different letters* indicate significant differences between treatments at P<0.05. CK – control, and salt treatments: 0.1 mol L^{-1} (ST1), 0.3 mol L^{-1} (ST2), and 0.5 mol L^{-1} (ST3).

Table 3. Changes of absorption flux per reaction center (RC) (ABS/RC), dissipated energy flux per RC (DI_0/RC), trapped energy flux per RC (TR_0/RC), electron transport flux per RC (ET_0/RC) of *Lycium ruthenicum* Murr. seedlings under control (CK), and salt treatments: 0.1 mol L^{-1} (ST1), 0.3 mol L^{-1} (ST2), and 0.5 mol L^{-1} (ST3). Data are means ± SE (n = 5). *Different letters* indicate significant differences between treatments at P<0.05. DAE – days of experiment.

Treatment	DAE	ABS/RC	DI_0/RC	TR_0/RC	ET_0/RC
CK	0	2.25 ± 0.04^a	0.31 ± 0.01^a	1.65 ± 0.03^a	0.94 ± 0.01^a
	7	2.27 ± 0.15^a	0.30 ± 0.03^a	1.65 ± 0.05^a	0.97 ± 0.05^a
	14	2.21 ± 0.08^a	0.32 ± 0.02^a	1.66 ± 0.03^a	0.97 ± 0.01^a
	21	2.26 ± 0.14^a	0.31 ± 0.02^a	1.63 ± 0.03^a	0.93 ± 0.06^a
ST1	0	2.22 ± 0.12^a	0.31 ± 0.02^a	1.65 ± 0.09^a	0.94 ± 0.02^{ab}
	7	2.36 ± 0.09^{ab}	0.34 ± 0.01^a	1.70 ± 0.02^a	0.82 ± 0.06^a
	14	2.48 ± 0.16^{ab}	0.43 ± 0.04^b	1.75 ± 0.11^a	1.03 ± 0.02^b
	21	2.62 ± 0.05^b	0.48 ± 0.06^b	1.82 ± 0.03^a	0.96 ± 0.07^b
ST2	0	2.27 ± 0.15^a	0.31 ± 0.00^a	1.64 ± 0.01^a	0.91 ± 0.02^a
	7	2.48 ± 0.07^a	0.48 ± 0.04^{ab}	1.72 ± 0.02^a	0.91 ± 0.07^a
	14	2.66 ± 0.10^b	0.54 ± 0.13^{ab}	1.87 ± 0.11^b	1.08 ± 0.05^b
	21	2.86 ± 0.05^b	0.73 ± 0.10^b	1.96 ± 0.02^b	1.07 ± 0.03^b
ST3	0	2.20 ± 0.03^a	0.30 ± 0.00^a	1.65 ± 0.04^a	0.94 ± 0.01^a
	7	2.54 ± 0.10^a	0.53 ± 0.07^a	1.96 ± 0.06^b	0.96 ± 0.06^b
	14	3.32 ± 0.14^b	1.07 ± 0.12^b	2.25 ± 0.06^c	1.14 ± 0.02^c
	21	3.68 ± 0.30^b	1.40 ± 0.27^b	2.27 ± 0.07^c	0.92 ± 0.06^c

constant in CK but increased with increasing salinity and stress duration (Table 2). The F_0 values in the CK and salt stress-treated plants were significantly different after 7 DAE. F_m decreased in the salt-stressed groups with increasing stress duration. After 7 DAE, the F_m values in the salt-stressed plants were significantly different from

Table 4. Changes of dissipated energy flux per cross section (CS) (DI_0/CS_0), trapped energy flux per CS (TR_0/CS_0), electron transport flux per CS (ET_0/CS_0), and amount of active PSII reaction centers per CS (RC/CS_0) of *Lycium ruthenicum* Murr. seedlings under control (CK), and salt treatments: 0.1 mol L^{-1} (ST1), 0.3 mol L^{-1} (ST2), and 0.5 mol L^{-1} (ST3). Data are means ± SE (n = 5). *Different letters* indicate significant differences between treatments at P<0.05. DAE – days of experiment.

Treatment	DAE	DI_0/CS_0	TR_0/CS_0	ET_0/CS_0	RC/CS_0
CK	0	37.29 ± 2.70[a]	182.75 ± 6.71[a]	104.89 ± 13.13[a]	105.36 ± 8.81[a]
	7	34.05 ± 3.47[a]	183.75 ± 6.46[a]	106.94 ± 9.62[a]	106.77 ± 6.92[a]
	14	37.22 ± 2.59[a]	186.18 ± 26.82[a]	110.44 ± 3.98[a]	103.42 ± 10.02[a]
	21	39.64 ± 2.59[a]	187.77 ± 6.22[a]	109.93 ± 12.81[a]	106.61 ± 2.57[a]
ST1	0	33.27 ± 3.57[a]	182.15 ± 2.48[a]	108.80 ± 4.38[a]	103.31 ± 2.53[a]
	7	45.43 ± 1.40[a]	183.77 ± 3.43[a]	89.78 ± 5.50[a]	85.99 ± 12.05[a]
	14	50.75 ± 4.38[a]	220.05 ± 8.42[b]	132.21 ± 8.42[a]	124.34 ± 16.97[a]
	21	52.96 ± 10.81[a]	186.91 ± 6.84[a]	95.88 ± 6.78[b]	168.43 ± 21.21[b]
ST2	0	33.72 ± 1.64[a]	180.93 ± 1.16[a]	106.52 ± 9.75[a]	103.47 ± 2.85[a]
	7	50.97 ± 4.27[b]	199.20 ± 9.59[a]	108.10 ± 6.03[a]	120.36 ± 9.55[a]
	14	64.54 ± 7.67[b]	229.12 ± 8.88[b]	133.77 ± 8.94[a]	141.25 ± 12.76[a]
	21	80.49 ± 5.47[c]	195.25 ± 13.21[a]	115.45 ± 11.45[a]	204.24 ± 24.12[b]
ST3	0	33.02 ± 0.68[a]	180.98 ± 5.08[a]	103.12 ± 1.99[a]	102.11 ± 1.40[a]
	7	63.20 ± 2.57[b]	209.63 ± 11.48[ab]	102.51 ± 9.04[a]	104.50 ± 5.73[a]
	14	109.08 ± 11.47[c]	231.66 ± 24.23[b]	108.78 ± 8.31[a]	106.75 ± 7.41[a]
	21	133.90 ± 24.82[d]	217.90 ± 10.49[ab]	88.45 ± 8.30[a]	137.67 ± 13.55[b]

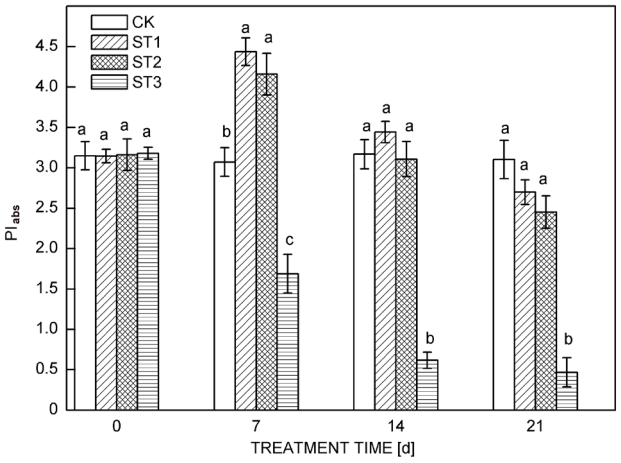

Fig. 4. Performance index on absorption basis (PI_{abs}) of control and salt-treated Lycium ruthenicum Murr. seedlings. Data are means ± SE (n = 5). *Different letters* indicate significant differences between treatments at P<0.05. CK – control, and salt treatments: 0.1 mol L^{-1} (ST1), 0.3 mol L^{-1} (ST2), and 0.5 mol L^{-1} (ST3).

that of CK. F_v/F_m decreased in salt-stressed groups with increasing salinity and stress duration. At 21 DAE, the F_v/F_m values of ST3 decreased by 4.9, 13.6, and 22.2% of the values for CK, ST1, and ST2, respectively. The V_j values increased with increased salinity and stress duration and were significantly different from that of CK after 7 DAE.

Flux ratio parameters: The value of φ_{PO}, which is the maximal photochemical efficiency of PSII, decreased with increasing salt concentration and stress duration (Fig. 3*A*). At 21 DAE, the value in ST3 decreased by 21.8, 15.9, and 13.8% compared to those of CK, ST1, and ST2, respectively. φ_{EO}, the quantum yield for electron transport, decreased with increasing salt concentration and stress duration (Fig. 3*B*). At 21 DAE, ST3 decreased by 48.2, 43.0, and 35.9% compared to those of CK, ST1, and ST2, respectively. ψ_o is the probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A. The ψ_o values remained constant in CK and decreased under salt stress treatment with increasing salt concentration and stress duration. At 21 DAE, ψ_o in CK was higher by 7.3, 19.1, and 34.7% than that of ST1, ST2, and ST3, respectively (Fig. 3*C*). φ_{DO} is the maximum primary photochemistry quantum yield. φ_{DO} values increased with increasing salt concentration and stress duration, with the value of ST3 increasing by 92.4, 48.4, and 37.9% compared to those of CK, ST1, and ST2, respectively (Fig. 3*D*) at 21 DAE.

Energy fluxes per reaction center: The values of ABS/RC, DI_0/RC, and TR_0/RC increased with increasing salt concentration and stress duration (Table 3). In ST3, the ABS/RC, DI_0/RC, and TR_0/RC values increased significantly. At 21 DAE, the ABS/RC values of ST3 increased by 62.4, 40.4, and 28.4% compared to those of CK, ST1, and ST2, respectively. The DI_0/RC values of ST3 increased 3.52, 1.94, and 0.93 times of those of CK, ST1, and ST2, respectively, at 21 DAE. ET_0/RC values showed no significant difference between all treatments and treatment times.

Phenomenological flux per cross section: DI_0/CS_0 values increased significantly under salt stress treatment

(Table 4). In ST3, DI_0/CS_0 values increased 0.17, 0.59, 1.39, and 3.18 times at 0, 7, 14, and 21 DAE, respectively, compared with those of CK. The TR_0/CS_0 values also increased with increasing salt stress concentration. At each salt concentration, the TR_0/CS_0 values reached the maximum at 14 DAE.

ET_0/CS_0 values initially increased and subsequently decreased with increasing salt concentration and stress duration, reaching the maximum value at 14 DAE. The RC/CS_0 values increased with increasing salt concentration and stress duration. In ST2, RC/CS_0 values reached the maximum at 14 to 21 DAE.

Photosynthetic performance index: The PI_{abs} values remained constant in CK and decreased gradually with increasing stress duration and salt concentration (Fig. 4). At 21 DAE, the PI_{abs} values of ST3 decreased by 85.0, 82.7, and 81.0% compared to those of CK, ST1, and ST2, respectively. At 21 DAE, the PI_{abs} values of CK, ST1, ST2, and ST3 decreased by 1.4, 14.2, 22.5, and 85.3% compared to 0 DAE, respectively.

Discussion

In this study, we found that *L. ruthenicum* seedlings exhibited strong salt tolerance. The seedling growth and dry mass production of *L. ruthenicum* were insensitive to mild and moderate salt stresses (Fig. 1). Under mild and moderate salt-stress treatments, seedling height, base diameter, crown, leaf mass, stem mass, and root mass increased with increasing salt concentration and reached the maximum in ST2. Mild and moderate salt stresses were beneficial to *L. ruthenicum* seedling growth. Similar results were reported in *Sophora japonica* L. (Zhang *et al*. 2002), *Acer palmatum* (Tang *et al*. 2015), and *Beta vulgaris* (Choi *et al*. 2016). With further increase of the salt concentration in soil, the growth of *L. ruthenicum* seedlings became limited. Under the salt stress treatment, roots are the first organ to experience adverse stress signal and produce corresponding physiological changes. With the increase in salt concentration, the *L. ruthenicum* seedling showed relatively increased allocation of dry matter to the roots. In addition, root length and R:S gradually increased. Under further stress, the main root length and root dry mass decreased. Similar results were reported in *Suaeda glauca* (Yi *et al*. 2011) and *Quercus virginiana* (Wang *et al*. 2014). Changes in Chl fluorescence can respond to environmental factors affecting plants. The analysis of a rapid Chl fluorescence kinetic curve under different environmental conditions can facilitate an in-depth understanding of the effect of environmental factors on PSII reaction center, plant photosynthetic mechanism adaptation mechanism of photosynthetic apparatus to environment. Rapid Chl fluorescence induced a kinetic curve, which included O, J, I, and P. V_j change indicated the continuous reduction of the electron acceptor, and the PSII reaction center started closing. Phase O represents a situation where all molecules of the primary electron acceptor of PSII (Q_A) are in the oxidized state (Xu *et al*. 2015). During transition from phase O to phase J, Q_A was restored to Q_A^-. The V_j value increased slowly under ST1 and ST2, the results showed that electron transport was blocked at PSII donor and acceptor side. The V_j value increased significantly under ST3, which showed that salt stress damaged the electron transport of PSII acceptor side, therefore, the growth of *L. ruthenicum* seedlings was inhibited at ST3.

This study showed that with the increasing salt concentration, the F_0 value of *L. ruthenicum* increased and the F_m value gradually decreased. F_0 value at ST3 was higher than that of CK, ST1, and ST2. The results indicated that the leaves of *L. ruthenicum* suffered from photoinhibition and PSII was damaged, and PSII excitation energy distribution changed under salt stress. However, *L. ruthenicum* seedlings improved their heat dissipation to consume excessive excitation energy to adapt under salt-stress environment at ST1 and ST2. Under ST3, salt stress decreased electron transfer rate, which caused reversible inactivation of PSII reaction center. Similar results were reported by Li *et al.* (2013), Yang *et al.* (2013), and Guo *et al.* (2016).

Chl fluorescence induction kinetic parameters are the important indexes to examine the extent of stress injury. ABS/RC, DI_0/RC_0, TR_0/RC_0, and ET_0/RC values increased significantly under salt stress mainly due to efficient enhancers of single reaction centers. In the process, the light energy of absorption and trapping did not increase the energy of ET_0/CS_0 during electron transport in unit area and increased the DI_0/RC and DI_0/CS_0 values. The results showed that the light energy of absorption and trapping ensured electron transport, while heat facilitated the largest dissipation. Similar results were reported in *Ginkgo biloba* (Wei *et al.* 2012). The self-protection mechanisms of *L. ruthenicum* seedlings under salt-stress treatment were as follows: the φ_{PO} value decreased with the increasing salt concentration, whereas φ_{DO} increased gradually. The electron transport capacity of PSII donor side was inhibited under salt stress, and the ψ_o and φ_{EO} values were lower than that of CK. Similar results were reported in *Capsicum annuum* L. var. *grossum* (Zhang *et al.* 2016). F_v/F_m can indicate the response of plant to stress. F_v/F_m gradually decreased under salt stress. The result showed that *L. ruthenicum* seedlings were suppressed by light. The PI_{abs} is the parameter, which reflects the overall status of photosynthetic apparatus (Stirbet *et al.* 2018). Under ST3, the PI_{abs} value of salt stress-treated plants was significantly lower than that of CK. The results showed that leaf photosynthesis was influenced by severe salt stress.

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