The response of photosynthetic functions of F_1 cutting seedlings from *Physocarpus amurensis* Maxim (♀) × *Physocarpus opulifolius* "Diabolo" (♂) and the parental leaves to saline stress

Xu Nan[1], Zhong Haixiu[1], Xin li[2], Yin ZePeng[3], Zhu Wenxu[3], Zhang Huihui[2,*]

[1] Natural Resources and Ecology Institute, Heilongjiang Academy of Sciences, Harbin, 150040, China
[2] College of Resources and Environment, Northeast Agricultural University, Harbin, Heilongjiang Province, 150030, China
[3] College of Resources and Environment, Shen Yang Agricultural University, Shenyang, Liaoning Province, 110866, China
* Correspondence:xtwfwf@126.com

Abstract: This paper selected clonal cutting seedlings from the F_1 hybrid varieties of *Physocarpus amurensis* Maxim (♀) × *Physocarpus opulifolius* "Diabolo" (♂) as research material to study the response of the photosynthetic gas exchange parameters and chlorophyll fluorescence parameters of *Physocarpus amurensis* hybrids and their parental leaves to NaCl stress (with concentrations of 0, 50, 100 and 200 mmol·L^{-1}). The results showed that under saline stress, the stomatal conductance (G_s), transpiration rate (T_r), and net photosynthetic rate (P_n) of the three kinds of *P. amurensis* all significantly decreased. When the NaCl concentration was below 100 mmol·L^{-1}, the intercellular CO_2 concentration (C_i) of leaves of the three samples declined with the increase of salt concentration; however, when the concentration increased to 200 mmol·L^{-1}, C_i did not decrease significantly, especially when the C_i of *P. opulifolius* "Diabolo" presented a slight increase. This indicated that the decline of photosynthetic carbon assimilation capacity induced by saline stress was the consequence of interaction between stomatal factors and non-stomatal factors, and the non-stomatal factors played an important role when the saline concentration was below 200 mmol·L^{-1}. Compared with *P. amurensis*, the photosynthetic gas exchange capability of *P. opulifolius* "Diabolo" leaves was more sensitive to saline stress, and the limitation of non-stomatal factors was relatively evident, but the photosynthetic capacity of hybrid *Physocarpus amurensis* Maxim leaves with the desired purple color was improved compared with *Physocarpus amurensis*. Under saline stress, the PSII activity of the three kinds of *P. amurensis* leaves declined, the electron transfer was inhibited, and obvious signs of photoinhibition were present. The PSII activity of *P. opulifolius* "Diabolo" leaves was more sensitive to saline stress than in *Physocarpus amurensis*. Under saline stress, the *NPQ* of *P. opulifolius* "Diabolo" leaves decreased greatly, while under high saline concentrations the degree of photoinhibition in *Physocarpus amurensis* and hybrid *P. amurensis* were reduced due to a relatively high *NPQ*. With the increase of saline concentration, the V_k of *P. amurensis* and hybrid *P. amurensis* leaves presented a decreasing trend, but the V_k of *P. opulifolius* "Diabolo" leaves increased slightly. This suggested that the effects of saline stress on the oxygen-evolving complex (OEC) of the three *P. amurensis* sample types were relatively limited and only the OEC of *P.s opulifolius* "Diabolo" leaves were slightly sensitive to saline stress. The V_j of all the leaves of the three *Physocarpus amurensis* types increased under saline stress, and increased significantly when the saline concentration increased to 200 mmol·L^{-1}, indicating that saline stress obviously impeded the electron transfer chain from Q_A to Q_B on the PSII receptor side of the leaves. Moreover, high saline concentrations would cause thylakoid membrane dissociation. The electron transfer and degree of damage to the thylakoid membrane of *P. opulifolius* "Diabolo" leaves were obviously higher than that of *P. amurensis*, but the electron transfer capacity on the PSII receptor side as well as the degree of damage of the thylakoid membrane of hybrid *P. amurensis* leaves were obviously lower than those of *P. opulifolius* "Diabolo." The salt tolerance of photosynthetic functions of hybrid *Physocarpus amurensis* (♀) × *Physocarpus opulifolius* "Diabolo" (♂) leaves was improved compared with that of parental *Physocarpus opulifolius* "Diabolo," and the hybrid shows obvious hybrid vigor in the aspect of photosynthesis.

Keywords: *Physocarpus amurensis* Maxim; *Physocarpus opulifolius* "Diabolo"; hybrid; saline stress; photosynthetic characteristics; chlorophyll fluorescence characteristics

Introduction

Saline stress is an important factor limiting plant growth and development, especially under the current expansion of saline alkaline lands and gradual deterioration of the degree of salinity. Therefore, developing salt tolerant hybrids is vital to remediation of saline-alkaline vegetation as well as urban afforestation. Photosynthesis is the foundation of guaranteeing normal plant growth and development under environmental stress. Besides the direct toxic effect of

saline ions to plants, saline stress will also result in osmotic stress and oxidative damage (*Liang & Wang, 2009; Munns, 2002*). Saline stress will inhibit plant growth through influencing the photosynthetic capacity of plants (*Ma et al., 1997*). For example, the photosynthetic capacity of glycophyte plants, such as barley and wheat, was obviously inhibited by saline stress (*Yang et al., 2009; Yang et al., 2008a*). However, the photosynthetic capacity of the halophyte *Chloris virgata* was not impeded by higher saline-alkali stress (*Yang et al., 2008b*). Saline stress will inhibit the activity of the PSII reaction center in plant leaves. For example, the declining activity of OEC on the PSII electron donor side and degradation of proteins on the PSII electron receptor side will influence the electron transfer on the PSII acceptor side (*Zhang et al., 2013; Sharkey & Badger, 1982*). The decrease of the electron transport rate will result in the accumulation of surplus electrons in the electron transport chain; thereafter, electron leak will attack free oxygen molecules in the cells and lead to burst out of reactive oxygen species (ROS) and also accelerate the degree of damage of the PSII reaction center (*Chen et al., 2010)*, or even lead to the peroxidation or dissociation of thylakoid membranes (*Mitsuya et al., 2000*).

Hybrid vigour is a ubiquitous biological phenomenon (*Prasd et al., 1994; Yu & Yin, 2010*). Numerous studies have shown that the growth of hybridal plants, photosynthetic capacity, and the adaptability to stress were all better than those of parental plants (*Dong et al., 2017*). *Ye et al. (2002)* explained in the photosynthetic superiority hypothesis of the forest hybrid vigor that the origin of forest hybrid vigour was the common response to natural stress and the difference in adaptability in hybrid and parental plants, among which the difference of photosynthesis was the most important (*Ye & Wang, 2002*). The photosynthetic capacity *Sorghum bicolor* × *S. sudanense,* which was derived from *Sorghum sudanense* (Piper) Stapf and *Sorghum bicolor* (L.) Moench, had a higher photosynthetic capacity than *Sorghum sudanense* as well as better adaptability under drought stress (*Zhang et al., 2012*). The hybrid F1 generation of *Ipomopsis aggregate*x *Ipomopsis tenuituba* showed higher hybrid vigour in the photosynthetic capacity at different phases than parental plants (*Campell et al., 2005*). The adaptability of the hybrid variety derived from *Iirises fulva* and *Iirises hexagona* to stress was obviously better than the parental plants (*Burke et al., 1998*). The hybrid offspring of *Helianthus annuus* and *Helianthus petiolaris* also had a higher adaptability than the parental plants *(Whitney et al, 2010*).

Except for the *Physocarpus amurensis* Maxim, the genus *Physocarpus* includes species with colorful leaves appropriate for horticulture such as *Physocarpus opulifo lius* 'Lutein*"* and *Physocarpus opulifolius* "Diabolo". *Physocarpus* species have graceful forms, are good ornamentals, and are also are rich in triterpenoids with anti-tumor effects, thus are important economically (*Zhang et al., 2016; Zhou et al., 1986*). Due to factors such as weak pollen viability and anthropogenic habitat destruction of *Physocarpus*, its distribution range and population size has decreased and has been listed as endangered plants in China (*Yin et al., 2010; Qin et al., 1993*). *Physocarpus opulifolius* "Diabolo" is a purple-leaf ornamental plant belonging to the *Physocarpus* genus, which is an ornamental flowering shrub that was recently introduced from North America *(Liu & Yu, 2011; Zhang et al., 2017*). Although *Physocarpus opulifolius* "Diabolo" has morphological and reproductive advantages, its stress resistance is relatively weak. In the cold areas of Northern China, its spring green up is relatively slow and its drought resistance is relatively lower than *P. amurensis* (*Xu et al., 2017*). Hybrid plants a have stronger photosynthetic capacity, which is one of the main aspects of hybrid vigour (*Li et al., 2012; Huang et al., 2013*). During 2006–2009, *Yu et al.* (2010) from the Forest Botanical Garden of Heilongjiang Province successfully obtained 202 plants of F1 seedlings from the hybrid of local *Physocarpus amurensis*(♀) × *Physocarpus opulifolius* "Diabolo" (♂), among which 88 plants had seedling leaf color identical or similar to the F1 hybrid *P. amurensis* of parental plants. The 88 F1 *P. amurensis* hybrid individuals not only had the ornamental quality desired of *Physocarpus opulifolius* "Diabolo" but also grew vigorously with a uniform canopy, presented stronger cold tolerance, and the development of hibernacles was drastically earlier than that of local *P. amurensis*. Our previous studies have found that although *P. opulifolius* "Diabolo" had good ornamental qualities, its saline tolerance was significantly lower than that of local *P. amurensis*. Compared with *P. amurensis* with stronger saline tolerance, it remains a question whether the obtained *P. opulifolius* hybrid with purple leaves had an advantage regarding saline tolerance. Therefore, by selecting cutting seedlings of the F1 generation of hybrid *P. amurensis* with better growth and purple leaves as experiment material, and the native *P. amurensis* (♀) and the imported *P. opulifolius* "Diabolo" (♂) from North America as controls, this study researches the response of leaf photosynthetic characteristics of hybrid *P. amurensis* and its two parental varieties to saline stress in order to enrich

the theoretical foundation of hybrid vigour for *P. amurensis* and provide fundamental data for reasonable planting and promotion of *Physocarpus*.

Materials and methods

Experiment materials and treatments

The experiment was carried out in the plant-physiology laboratory of the Northeast Forestry University from July to September in 2016, and the experiment materials were three-year-old cutting seedlings of triennial *Physocarpus amurensis*, *Physocarpus opulifolius* "Diabolo", and the F1 hybrid *Physocarpus amurensis* (♀) × *Physocarpus opulifolius* "Diabolo" (♂) with purple leaves, which were provided by Heilongjiang Forest Botanical Garden. The two parents and F1 hybrid had three–five branches and were about 0.3–0.5 m. The seedlings were planted in plastic flower pots with an opening diameter of 28 cm, bottom diameter of 15 cm, and height of 20 cm. Each pot was planted with one plant and the cultivating matrix was turfy soil. On July 20th, 2016, the three sample types were irrigated with NaCl solutions with four concentrations, i.e., 0 (CK), 50, 100, and 200 mmol·L^{-1} to conduct the saline stress tests. Each pot was irrigated with 1 L of solution and one tray was connected with each pot so that the percolated NaCl solution can be returned to the pot in time. One week after saline treatment, the photosynthetic gas exchange parameters and chlorophyll fluorescence parameters were measured after the salt damage of leaves among the treatments showed differences.

Measurements and methods

The measurement of photosynthetic gas exchange parameters: At 10:00 a.m. one week after saline treatment, the Li-6400 photosynthesis measurement system was utilized to fix the light intensity of 1,000 μmol·m^{-2}·s^{-1} and CO_2 concentration of 400 μL·L^{-1}. For each treatment, the third or fourth last fully expanded leaf on the current-year new shoot was selected to measure the photosynthetic gas exchange parameters such as net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (T_r), and cellular CO_2 concentration (C_i).

The measurement of chlorophyll fluorescence parameters: The third or fourth last fully expanded leaf of *Physocarpus amurensis* Maxim seedlings of different treatments were processed with 0.5 h of dark adaption using the dark adaption clamps. Following the methods described in *Hu et al.* (2007), a portable pulse modulated fluorometer FMS-2 (Hansatch Co., UK) was utilized to measure the PSII maximum photochemical efficiency (F_v/F_m), actual photochemical efficiency (Φ_{PSII}), photochemical quenching coefficient (φ_P), and non-photochemical quenching (NPQ). This measurement for each treatment was repeated three times.

The measurement of fast chlorophyll fluorescence induction kinetics curve: The Handy-PEA continuous stimulus fluorometer (Handy, UK) was utilized to measure the fast chlorophyll fluorescence induction kinetics curve (OJIP fluorescence induction curve) of the 3rd or 4th last fully expanded leaf of different plants. Before measurement, the leaves were processed with dark adaption for 30 min. The four characteristic points, O, J, I, and P, were the points corresponding to moment 0, 20, 30, and 1,000 ms on the OJIP curve, and their corresponding relative fluorescence intensities were denoted with F_o, F_J, F_I, and F_m, respectively. The 0.15 and 0.3 ms moments on the OJIP curve were defined as L and K, and their corresponding relative fluorescence intensity were denoted with F_L and F_K, respectively. The standardization of the OJIP curves of different treatments should be processed with O-P, O-J, and O-K; the relative fluorescence intensity at point O was defined as 0, and point P, J, and K were defined as 1 for standardization. The standardization equation was $V_{O-P} = (F_t-F_o)/(F_P-F_o)$, $V_{O-J} = (F_t-F_o)/(F_J-F_o)$, and $V_{O-K} = (F_t-F_o)/(F_K-F_o)$, respectively. In the equations above, F_t was the relative fluorescence intensity at different time points, and the three characteristic points L, K, and J of the standardized curves were denoted with V_L, V_K, and V_J, i.e., $V_L = (F_L-F_o)/(F_K-F_o)$, $V_K = (F_K-F_o)/(F_J-F_o)$, and $V_J = (F_J-F_o)/(F_P-F_o)$. The difference was calculated between V_{O-P}, V_{O-J}, and V_{O-K} curves of plant leaves under different saline concentrations, and CK curve, which was indicated as $\triangle V_{O-P}$, $\triangle V_{O-J}$ and $\triangle V_{O-K}$ (*Strasser et al., 1995; Zhang et al., 2011*).

Data processing method

Excel (2003) and SPSS (22.0) software were employed to conduct statistical analyses, and one-way analysis of variance (one-way ANOVA) and least significant difference (LSD) tests were employed to compare the difference among different data groups.

Results and analyses

The effect of saline stress on the photosynthetic gas exchange parameters of leaves of three *Physocarpus*

***amurensis*varieties**

Under non-saline stress, the P_n, G_s, and T_r of *P. opulifolius* "Diabolo" leaves were all slightly higher than those of *P. amurensis* and hybrid *P. amurensis* (Fig1A, 1B, 1C and 1D) However, with the increasing salt concentration, the decreasing rate of the P_n, G_s, and T_r of *P. opulifolius* leaves was obviously greater than that of *P. amurensis* and hybrid *P. amurensis*. Moreover, P_n, G_s, and T_r of *P. amurensis* and hybrid *P. amurensis* showed insignificant difference under different salt concentrations. Overall, with the increase of salt concentration, the C_i of three sample types of *Physocarpus* leaves presented a declining trend and the difference between different varieties was relatively small. Yet, the C_i of *P. opulifolius* leaves under saline stress of 200 mmol·L^{-1} increased slightly compared with that under stress of 200 mmol·L^{-1}.

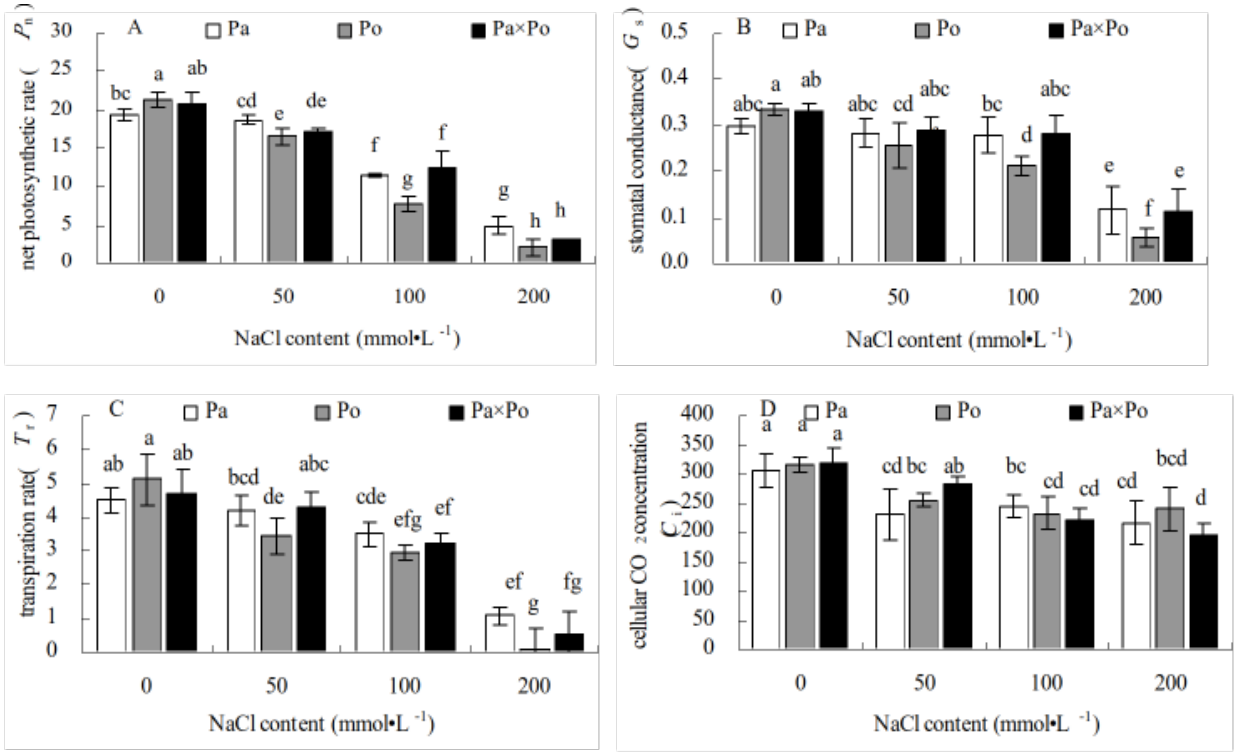

Fig. 1. The effect of saline stress on the photosynthetic gas exchange parameters of leaves of three *Physocarpus amurensis* varieties

Note: Pa: *Physocarpus amurensis* Maxim (♀), Po: *Physocarpus opulifolius* "Diabolo" (♂), Pa×Po: *Physocarpus amurensis* Maxim (♀) × *Physocarpus opulifolius* "Diabolo" (♂), Data in the figure are mean ±SE, values followed by different small letters mean significant difference ($p<0.05$)

The effect of saline stress on the chlorophyll fluorescence parameter of leaves of three Physocarpus amurensis varieties

Under non-saline stress, the chlorophyll fluorescence parameters of leaves of the three Physocarpus amurensis sample groups had no significant difference (Fig2A, 2B, 2C and 2D). With the increase of salt concentration, Fv/Fm, ΦPSⅡ, and qP of the three P. amurensis sample group leaves presented obvious declining trends, while NPQ presented an overall trend of increasing first and then decreasing. Under salt concentrations of 50 mmol·L-1, Fv/Fm, ΦPSⅡ, and qP of P. opulifolius "Diabolo" were slightly higher than those of P. amurensis and hybrid P. amurensis. The decreasing rates of Fv/Fm, ΦPSⅡ, and qP of P. opulifolius "Diabolo" under saline stress treatments of 100 and 200 mmol·L-1 were obviously greater than those of the other two samples. In addition, the NPQ of the leaves of the three P. amurensis sample groups under saline stress of different concentrations were all evidently higher than those not treated with saline stress. The NPQ of P. opulifolius "Diabolo" and hybrid P. amurensis leaves reached the highest under the concentration of 100 mmol·L-1, which significantly declined when the saline concentration rose to 200 mmol·L-1. However, the NPQ of P. amurensis did not show a decreasing trend, and the NPQ of P. opulifolius "Diabolo" under 200 mmol·L-1 decreased by 82.05% compared with that under 100 mmol·L-1, while the decreasing rate of hybrid P. amurensis was smaller (63.33%) than that of P. opulifolius "Diabolo".

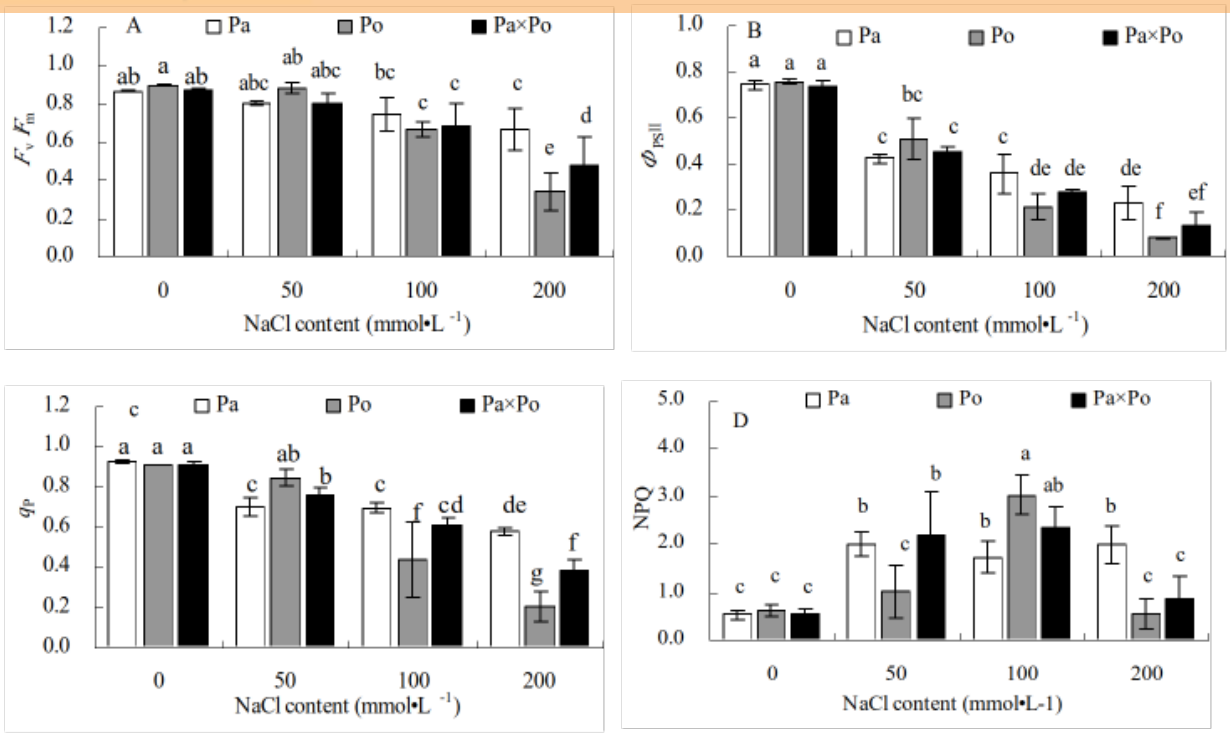

Fig. 2. The effect of saline stress on the chlorophyll fluorescenceparameters of leaves of three *Physocarpusamurensis*sample groups.

Note: Pa: *Physocarpus amurensis* Maxim (♀), Po: *Physocarpus opulifolius* "Diabolo" (♂), Pa×Po: *Physocarpus amurensis* Maxim (♀) × *Physocarpus opulifolius* "Diabolo" (♂), Data in the figure are mean ±SE, values followed by different small letters mean significant difference ($p<0.05$)

The effect of saline stress on the OJIP curves of leaves of the three *Physocarpusamurensis* sample groups

Compared with the OJIP curve of CK, the OJIP curve patterns of leaves of the three *Physocarpus amurensis* sample groups under saline stress of different concentrations had evident changes, which mainly presented as the following: the relative fluorescence intensity at point J, I, and P declined with the rising salt concentration, among which the declining extent at point P was the greatest; however, the relative fluorescence intensity at point O of leaves of the three *P. amurensis* sample groups under different concentrations had insignificant changes. The extent of decrease of the relative fluorescence intensity at point J, I, and P of *P. amurensis* treated with different saline concentrations was obviously smaller than those of *P. opulifolius* "Diabolo" and hybrid *P. amurensis*, and the decrease observed in *P. opulifolius* "Diabolo" was the greatest (Fig3A,3B and 3C).

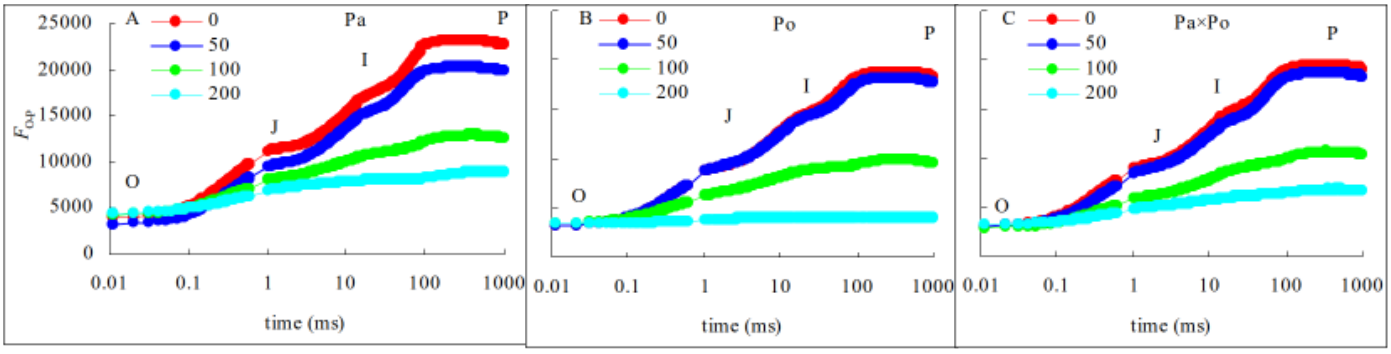

Fig. 3. The effect of saline stress on the OJIP curves of leaves of the three *Physocarpusamurensis*sample types.

The effect of saline stress on the standardized OJIP curves and V_J of leaves of the three *Physocarpusamurensis* sample types

After standardizing the OJIP curves of leaves of the three *P. amurensis* sample types under different treatments (Fig 4A, 4B, and 4C), we found that, compared with the CK treatment, the standardized OJIP curves of *P. amurensis* under the saline concentrations of 50 and 100 mmol·L^{-1} did not change significantly. However, when saline increased to 200 mmol·L^{-1}, the relative variable fluorescence at point J increased, while that of *P. opulifolius* "Diabolo" and hybrid *P.*

amurensis increased when the salt concentration reached 100 mmol·L^{-1}, and the extent of the increase of hybrid *Physocarpus amurensis* was slightly lower than that of *P. opulifolius* "Diabolo". Through calculating the difference between standardized OJIP curves under different concentrations and the CK curve (Fig 4D, 4E, and 4F), it could be seen that the relative variable fluorescence at various points of the three *Physocarpus amurensis* sample types under saline stress all presented the greatest at point J, and the extent of the increase was as follows: *Physocarpus opulifolius* "Diabolo" > hybrid *Physocarpus amurensis* > *Physocarpus amurensis*. Quantitative analysis of V_J under different saline concentrations (Fig. 4G) showed that under saline concentrations of 0 and 50 mmol·L^{-1}, the V_J of leaves of the three *P. amurensis* sample groups had no significant difference; however, under 100 and 200 mmol·L^{-1}, the V_J of *P. amurensis* was 12.41% ($P<0.05$) and 6.18% ($P<0.05$) lower than that of *P. opulifolius* "Diabolo" and hybrid *P. amurensis*, respectively, which have both reached a significant level. Although the V_J of hybrid *P. amurensis* was also higher than that of *P. amurensis*, the difference did not reach a significant level.

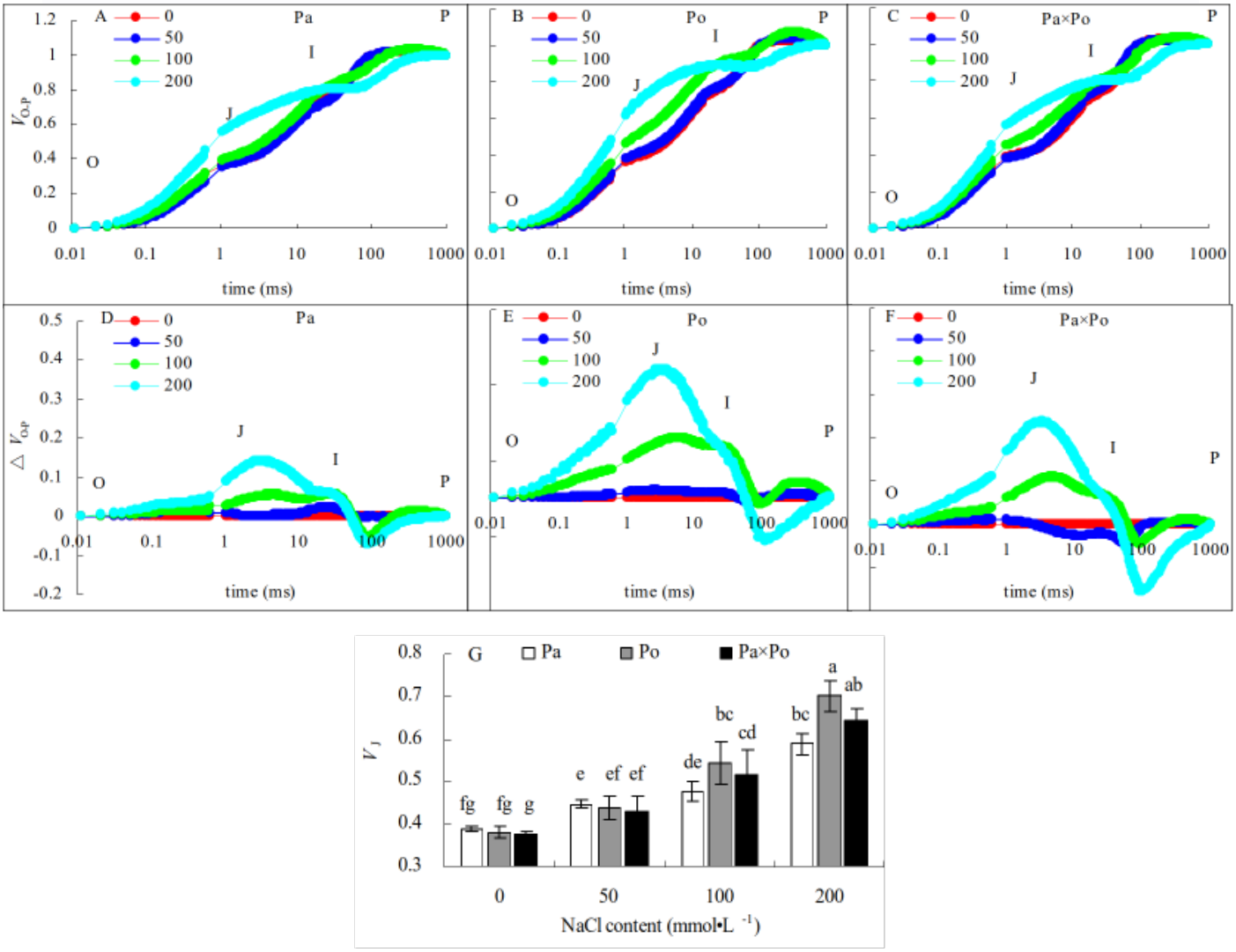

Fig. 4. The effect of saline stress on the standardized OJIP curves and V_J of leaves of three *Physocarpus amurensis* sample groups

Note: Pa: *Physocarpus amurensis* Maxim (♀), Po: *Physocarpus opulifolius* "Diabolo" (♂), Pa×Po: *Physocarpus amurensis* Maxim (♀) × *Physocarpus opulifolius* "Diabolo" (♂), Data in the figure are mean ±SE, values followed by different small letters mean significant difference ($p<0.05$)

The effect of saline stress on the standardized O–J curves and V_K of leaves of the three *Physocarpus amurensis* sample groups

By defining the relative fluorescence intensity of point O as 0 and that of point J as 1, we conducted O–J standardization of the curves of three *Physocarpus amurensis* sample types (Fig 5A, 5B, and 5C), and then subtracted the treatment results with the control (Fig 5D, 5E, and 5F). We found that under saline stress, the extent of change of standardized O–J curves of the three *P. amurensis* sample types was relatively small compared with that of CK. In

comparison with CK, at the point of about 0.5 ms of the O–J curve, the relative variable fluorescence (V_K) obviously decreased while that at the characteristic point of 0.3 ms. The extent of change was small, and only the V_K of *P. opulifolius* "Diabolo" under salt concentrations of 100 and 200 mmol·L^{-1} increased to some degree (Fig 5G). Quantitative analysis of V_K change of the three *P. amurensis* varieties under saline stress showed that, under non-saline stress, the V_K of *P. opulifolius* "Diabolo" leaves was significantly lower than that of *P. amurensis* and hybrid *P. amurensis*. However, with the increasing saline concentrations, the V_K of *P. amurensis* and hybrid *P. amurensis* obviously declined while that of *P. opulifolius* "Diabolo" increased a little, and the difference under different saline concentrations did not reach a significant level.

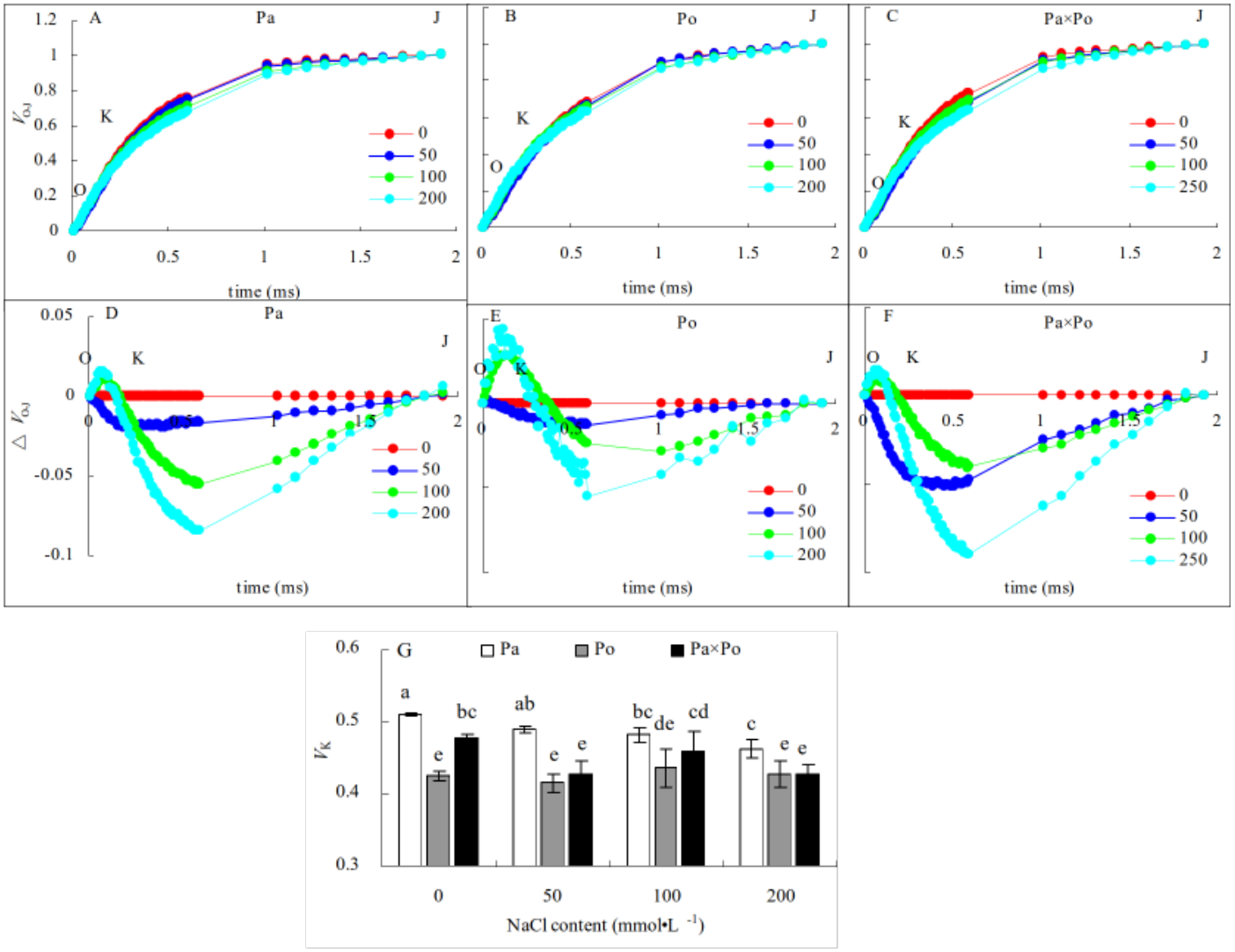

Fig. 5. The effect of saline stress on the standardized O–J curves and V_K of leaves from the three *Physocarpus amurensis* sample types.

Note: Pa: *Physocarpus amurensis* Maxim (♀), Po: *Physocarpus opulifolius* "Diabolo" (♂), Pa×Po: *Physocarpus amurensis* Maxim (♀) × *Physocarpus opulifolius* "Diabolo" (♂), Data in the figure are mean ±SE, values followed by different small letters mean significant difference ($p<0.05$)

The effect of saline stress on the standardized O–K curves and V_L of leaves from three *Physocarpus amurensis* sample types

The *P. amurensis* samples under saline stress had relative variable fluorescence (V_L) at 0.15 ms, i.e., point L of the standardized O–K curves presented evident differences (Fig. 6A, 6B, and 6C). By calculating the difference between standardized O–K curves and CK curves of the three *P. amurensis* sample types under saline stress (Fig. 6D, 6E, and 6F), the V_L of *P. amurensis* and hybrid *P. amurensis* under a saline concentration of 50 mmol·L^{-1} decreased slightly while that of *P. opulifolius* "Diabolo" did not change. However, under saline concentrations of 100 and 200 mmol·L^{-1}, V_L of leaves from three *P. amurensis* sample types all increased, and the increase in *P. opulifolius* "Diabolo" was the greatest. Under saline concentrations of 100 and 200 mmol·L^{-1}, the quantitative analysis of V_L change indicated that

the V_L of *P. opulifolius* "Diabolo" leaves was slightly higher than that of *P. amurensis* and hybrid *P. amurensis*, and their difference did not reach a significant level.

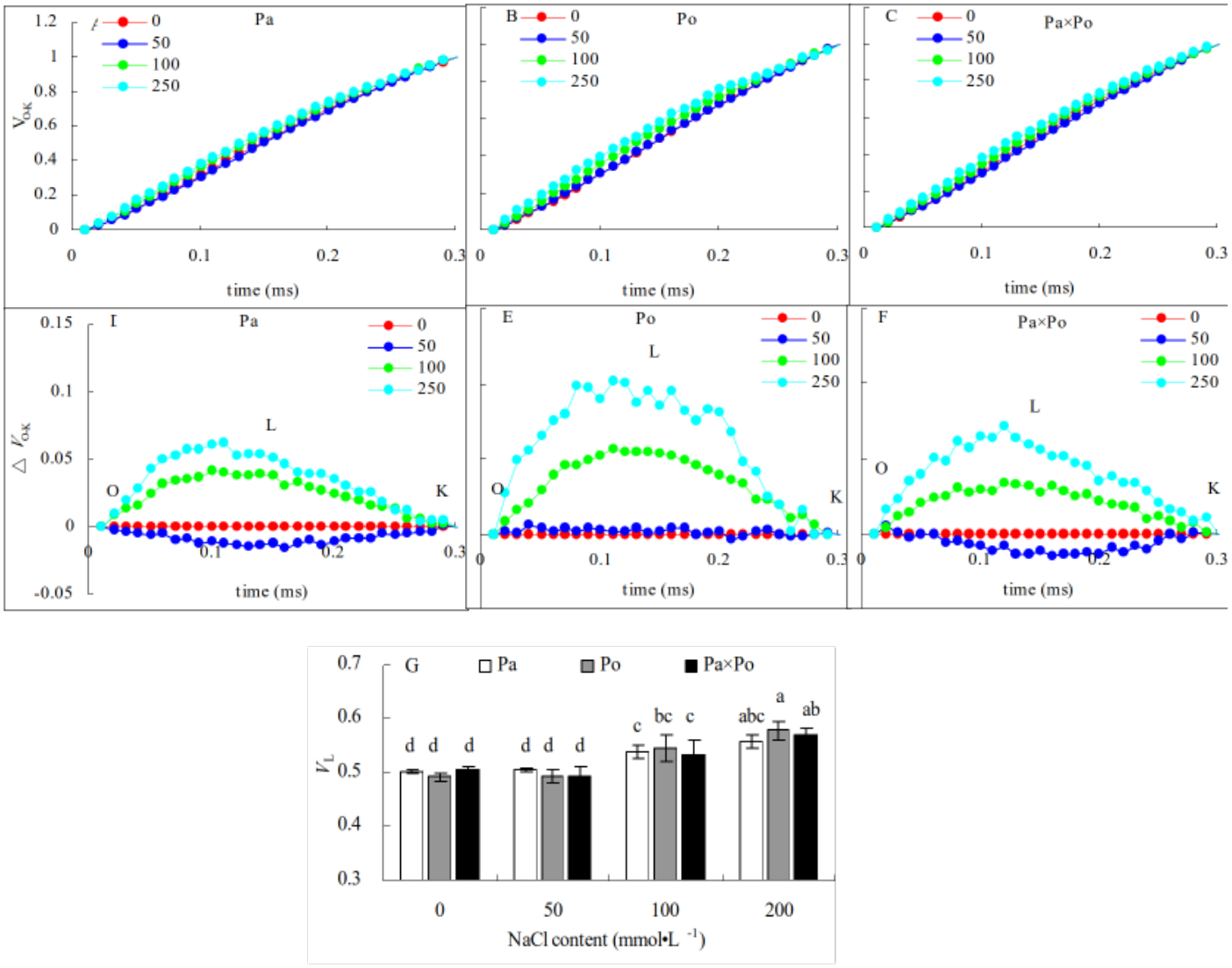

Fig. 6. The effect of saline stress on the standardized O–K curves and V_L of leaves from three *Physocarpus amurensis* sample groups.

Note: Pa: *Physocarpus amurensis* Maxim (♀), Po: *Physocarpus opulifolius* "Diabolo" (♂), Pa×Po: *Physocarpus amurensis* Maxim (♀) × *Physocarpus opulifolius* "Diabolo" (♂), Data in the figure are mean ±SE, values followed by different small letters mean significant difference ($p<0.05$)

Discussion

Photosynthesis is the foundation of plants acquiring materials and energy, and the strength of photosynthetic capacity has a very important effect on plant growth, production, and stress resistance (*Zhang et al., 2016*). Moreover, photosynthesis sensitive to stress (*Chaves et al., 2009*). With the increasing saline concentration, the stomatal conductance of leaves from three *P. amurensis* sample groups declined, which not only resulted in the decrease of the transpiration rate of leaves but also reduced the net photosynthetic rate of leaves; specifically, the photosynthetic carbon assimilation capacity was inhibited. Under different saline concentrations, the extent of the decrease of P_n, G_s, and T_r of *P. opulifolius* "Diabolo" and hybrid *P. amurensis* leaves were obviously greater than those of *P. amurensis*, which indicated that the saline tolerance of photosynthetic characteristics of *P. opulifolius* "Diabolo" was lower than that of *P. amurensis*. Although the photosynthetic gas exchange parameters of hybrid *P. amurensis* leaves were lower than those of *P. amurensis*, they were higher than those of *P. opulifolius* "Diabolo". The decrease of the photosynthetic carbon assimilation capacity under saline stress was related to stomatal and non-stomatal factors, the effect of which was relevant to the duration of saline stress and salt concentration (*Satoh et al., 1983; Wang et al., 2004*). In addition to saline ions directly inducing stomatal closure, stomatal factors were also connected with

physiological drought resulting from water potential decreasing in the matrix induced by saline stress. The non-stomatal factors might be the toxicity of saline ions reducing the CO_2 assimilation capacity in mesophyll cells and resulting in the accumulation of cellular CO_2 (*Zhang et al., 2012; Chen et al., 2009*). In this study, when the salt concentration reached 200 mmol·L^{-1}, although the G_s of the leaves from three *P. amurensis* sample groups obviously decreased, so did the P_n, but the C_i did not change, indicating that under highly saline stress the decrease of photosynthetic capacity was the result of co-limitation of both the stomatal factors and non-stomatal factors. The G_s of *P. opulifolius* "Diabolo" leaves was obviously lower than that of *P. amurensis* and hybrid *P. amurensis*, but the difference in C_i among the three sample types was not significantly different, indicating that the reason for inducing the decrease of photosynthetic capacity of *P. opulifolius* "Diabolo" was mainly due to non-stomatal factors. Furthermore, the CO_2 utilization capacity of *P. opulifolius* "Diabolo" mesophyll cells was sensitive to saline stress, while that of hybrid *P. amurensis* was improved to some extent.

Under saline stress, among all the non-stomatal factors, except for the CO_2 utilization capacity of mesophyll cells leading to the decrease of photosynthetic capacity, the decrease of PS II reaction center activity was also thought to be one of the important factors limiting photosynthetic capacity under saline stress (*Lu & Zhang, 2000*). In this study, with the increase of salt concentration, F_v/F_m, Φ_{PSII}, and q_P of leaves from the three *P. amurensis* sample groups all decreased significantly, indicating that under saline stress the PSII photochemical activity of the three sample groups declined and photo-inhibition was evident under high saline stress conditions. However, the degree of photo-inhibition of *P. amurensis* and hybrid *P. amurensis* under saline stress was obviously lower than that of *P. opulifolius* "Diabolo", and the extent of change of chlorophyll fluorescence parameters of hybrid *P. amurensis* leaves was also lower than in *P. opulifolius* "Diabolo", which indicated that hybridization with highly saline tolerant *P. amurensis* can evidently improve the salt tolerance of the PS II reaction center of hybrid *P. amurensis* leaves. If excessive light energy existed in plants under saline stress, the triplet state excited-state chlorophyll molecules produced from light excitation could react with the ground-state O_2 molecule and generate single-state oxygen, and reducing the formation of single-state oxygen can be realized through reducing the formation of triplet state chlorophyll or quenching of the existed triplet state chlorophyll. The formation of triplet state excited-state chlorophyll was inhibited by the xanthophyll cycle, and NPQ was positively correlated with heat dissipation depending on the xanthophyll cycle (*Li et al., 2000*). In this study, the NPQ of *P. amurensis* leaves under different salt concentrations were all higher than that of the CK treatment, i.e., *P. amurensis* can reduce the accumulation of excessive light energy within leaves under saline stress through increasing the xanthophyll cycle. However, the NPQ of *P. opulifolius* "Diabolo" and hybrid *P. amurensis* presented a trend of increasing first and then decreasing with the rising salt concentration, indicating that under low salt concentrations *P. opulifolius* "Diabolo" and hybrid *P. amurensis* can release the surplus light energy in time through starting the heat dissipation mechanism depending on the xanthophyll cycle, but the protective effect decreased under high saline stress. The NPQ of hybrid *P. amurensis* leaves under different salt concentrations were all higher than those of *P. opulifolius* "Diabolo", which indicated that the defensive mechanism of photo-damage of hybrid *P. amurensis* leaves under saline stress was increased compared with *P. opulifolius* "Diabolo".

The fast chlorophyll fluorescence kinetics curve was utilized to analyze the PSII injured sites of the leaves of the three *P. amurensis* sample types. The increase of the relative variable fluorescence at point K of 0.3 ms (V_K) was thought of as the specified symbol that the oxygen-evolving complex (OEC) on PSII electron donor side was injured (*Zhang et al., 2012*). The function of OEC was mainly involved in water splitting and oxygen release *(Guskov et al., 2009)*, and when the expression quantity of OEC decreased or its activity declined, the PSII activity of plant leaves decreased (*Brandle et al., 1977*). The OEC activity and expression quantity of proteins were obviously affected by saline stress (*Abbasi & Komatsu, 2004; Park et al., 2004*). The OEC protein expression quantity of *Medicago* Linn. Leaves under the stress of 100 mM NaCl did not change significantly, but when NaCl concentration was increased to 200 mM, the expression quantity declined significantly, which indicated that the protein expression might be related with the adaptability of *Medicago* to different saline stress concentrations (*Xiong, 2011*). *Allakhverdievet al. (2001)* found that 500 mM of NaCl would lead to the irreversible inactivation of *Synechococcus* OEC. However, studies also indicated that PSII OEC was located in the PSII lumen and it was made up of highly active Mn^{4+} clusters packed by three peripheral proteins, and Cl- can provide an ideal ionic environment for water oxidation (*Pang et al., 2010*). Our experimental results showed that with the increasing salt concentration, the V_K of *P. opulifolius* "Diabolo"

leaves increased slightly, but the V_K of *P. amurensis* and hybrid *P. amurensis* leaves presented a decreasing trend (Fig 5), which indicated that the effect of saline stress on the OEC of leaves from the three *P. amurensis* sample types was relatively small and it even enhanced the OEC activity of *P. amurensis* and hybrid *P. amurensis*. Therefore, the enhancement of OEC activity of *P. amurensis* leaves resulted from saline stress of NaCl was likely to be related with its Cl^- absorption. This result was consistent with the research results of Pang (*Zhang et al., 2016*) and Zhang (*Zhang et al., 2013*) that the OEC protein expression in *Arabidopsis*, *Thellungiella halophile*, and *Helianthus tuberosus* L. was up-regulated under saline stress.

Under saline stress, the blocked sites of PSII electron transference usually occurred on the electron receptor side of the PSII reaction center, and the electron transfer from Q_A (the primary electron receptor of the electron transfer chain of photosystem II) to Q_B (the secondary electron receptor of the electron transfer chain of photosystem II) were the main inhibited sites under saline stress (*Murata et al., 2007*). The D_1 protein was the PSII core protein combined with Q_B, which had a fast turnover and its synthesis and degradation in the photosynthetic electron transfer chain remained in a dynamic balance; once the degradation rate was higher than the synthesis rate, net degradation of the D_1 protein would happen and resulted in the decrease of F_v/F_m (*Takahashi & Murata, 2005*). Under the adverse conditions, the Calvin cycle and removal mechanism of reactive oxygen species (ROS) were inhibited in plant cells; the ROS content in chloroplasts would increase and then impeded the turnover of the D_1 protein, leading to blockage of PSII electron transfer and acceleration of photo-inhibition(*Cheng et al., 2016; Haldimann & Strasser, 1999).*The relative variable fluorescence at 2 ms of the OJIP curve, point J (V_J) represented the degree of closure of the active reaction center and the increase of V_J indicated that the electron transfer from Q_A to Q_B in the photosynthetic electron transfer chain was inhibited and the accumulation of redox-state Q_A gradually increased (*Venkatesh et al., 2012*). In this study, with the increase of salt concentration, the V_J of leaves from the three *P. amurensis* sample groups all increased, specifically the saline stress evidently inhibited electron transfer from Q_A to Q_B on the PSII electron receptor side. With the increasing salt concentration, the extent of increase of V_J in *P. opulifolius* "Diabolo" was evidently greater than that of *P. amurensis*, which meant that the electron transfer on the PSII electron receptor side of *P. opulifolius* "Diabolo" leaves was more sensitive to saline stress. However, the increase of V_J of hybrid *P. amurensis* was significantly lower than that of *P. opulifolius* "Diabolo", which showed that the saline tolerance of the electron transfer on the PSII electron receptor side of hybrid *P. amurensis* was improved compared with *P. opulifolius* "Diabolo", but whether it was related with the turnover of the D_1 protein needs further verification.

When electron transfer on the PSII electron transfer chain was blocked, the accumulation of excessive electrons leads to electronic leak and the leaked electrons will attack free O_2 within cells resulting in the formation of superoxide anions such as ROS (*Chen et al., 2005*). Reactive oxygen species are an important substance in plant cells and under normal physiological conditions, the ROS produced within cells can be removed rapidly by the scavenging system to prevent the oxidative damage of excessive ROS to cells. However, under adverse conditions the intracellular ROS will usually accumulate and then damage cells with strong oxidation (*Xu et al., 2000*). The ROS mediated by photosynthesis will first attack thylakoid membranes to accelerate its per-oxidation degree, and the peroxidation of thylakoid membranes will result in the decrease of PSII activity, blockage of electron transfer, and induction of the formation of more ROS, which forms a damaging cycle (*Nishiyama et al., 2011; Zhao et al., 2006*). Saline stress will induce the unsaturation of fatty acids in wheat thylakoid membranes (*Mcconn & Browse, 1998*), and severely affect thylakoid membranes functions (*Mitsuya et al., 2000*). *Mitsuya et al. (2000)* found that saline stress could cause the degradation of mesophyll thylakoid membrane of *Ipomoea batatas* Lam. Some studies also found that although saline stress could lead to the decrease of the electron transferring activity of PSII, oxygen evolving activity of chloroplasts and photosynthetic rate in rice leaves, it did not significantly influence the polypeptides in thylakoid membranes (*Yang et al., 2004*). This was mainly related to the salt concentrations of different treatments and the salt tolerance of different plant species. The increase of relative variable fluorescence of point L (V_L) was thought of as the change of thylakoid membrane fluidity, which was the major indicator that its structural and functional integrity was destroyed (*Essemine et al., 2012; De Ronde et al., 2005; Toth et al., 2005*). In this study, the V_L change of leaves from the three *P. s amurensis* sample groups under the saline stress of 50 $mmol \cdot L^{-1}$ was relatively small, and the V_L of *P.*

amurensis and hybrid *P. amurensis* leaves decreased slightly compared with the control, which indicated that the effect of 50 mmol·L^{-1} of saline stress on the thylakoid membranes of the three sample groups was small. However, with the further increase of salt concentrations, the degree of damage to the thylakoid membranes of the three sample types increased, especially in the thylakoid membrane dissociation of *P. opulifolius* "Diabolo", which was greater than that of *P. amurensis*, but dissociation of the thylakoid membrane of hybrid *P. amurensis* was evidently smaller than that of *P. opulifolius* "Diabolo".

Conclusion

The inhibition effect of saline stress on the photosynthesis of the three *P. amurensis* sample groups was the combined result of stomatal factors and non-stomatal factors. Among non-stomatal factors, the decrease of CO_2 utilization capacity of mesophyll cells and limited activity of the PSII reaction center were both important reasons. Under high-concentrations of saline stress, *P. amurensis* can reduce the production of excessive light energy by increasing *NPQ*, while the *NPQ* of *P. opulifolius* "Diabolo" was evidently reduced under high saline stress. Saline stress obviously inhibited the electron transfer capacity from Q_A to Q_B on the PS II receptor side, and resulted in the dissociation of thylakoid membranes to some extent, but its harm to the OEC activity on the PS II donor side was relatively limited. The hybrid variety of *P. amurensis*(♀) × *P. opulifolius* "Diabolo" (♂) not only maintained the desired purple leaves of *P. opulifolius* "Diabolo", but also inherited the stronger salt tolerance of the female parent, *P. amurensis*, and its salt tolerance in photosynthesis improved evidently compared with that of *P. opulifolius* "Diabolo".

Data Availability

The following information was supplied regarding data availability:
The research in this article did not generate any raw data.

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