



Full Length Article

Response of Chlorophyll Fluorescence Characteristics to Degraded Wetlands in the Leaves of *Carex lasiocarpa*, *C. pseudocuraica* and *Deyeuxia angustifolia* in the Wetland of Jilin Province, China

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Abstract

In this study, the changes in the function of photosystem II (PSII) in three dominant wetland plants as experimental materials under degraded wetlands were analyzed using chlorophyll fluorescence techniques. Leaf samples from three typical wetland plants, *Carex lasiocarpa*, *C. pseudocuraica* and *Deyeuxia angustifolia* in the Jilin Province wetland, China were used. The results showed that the net photosynthetic rate (P_n), transpiration rate (T_r) and stomatal conductance (G_s) of *C. pseudocuraica* and *D. angustifolia* were more higher significantly than *C. lasiocarpa*, and in intercellular CO_2 concentration (C_i) there was no significant difference. In addition, compared with *C. pseudocuraica*, *C. pseudocuraica* and *D. angustifolia* had higher photosynthetic performance index (PI_{ABS}) and PSII photochemical efficiency (F_v/F_m) based on absorption of light energy, indicating that the PSII photochemical activity of *C. pseudocuraica* and *D. angustifolia* is significantly higher than that of *C. lasiocarpa*. By standardizing the OJIP curve of leaves three dominant species in degraded wet ground, it can be found that the activity of oxygen evolving complex (OEC) on the donor side of PSII increased, and the electron transfer on the receptor side of PSII was significantly higher than that of *C. lasiocarpa*. The actual photochemical efficiency (Φ_{PSII}) and electron transfer rate (ETR) of *C. pseudocuraica* and *D. angustifolia* were also significantly higher than *C. lasiocarpa* under higher light intensity. In addition, through the utilization of PSII light energy, it can be found that the proportion of absorption of light energy dissipation in the form of invalid heat energy and the proportion of its distribution to the inactivation reaction center are reduced, while the absorption light energy was more used in the photochemical reaction center to improve its photochemical function. There was no significant difference in PSII function between the degraded wetland and the leaves of *C. pseudocuraica* and *D. angustifolia*, which indicated that the photosynthetic PSII function of *C. pseudocuraica* and *D. angustifolia* had strong adaptability to wetland degradation. © 2020 Friends Science Publishers

Key words: *Carex* spp.; *Deyeuxia angustifolia*; Degraded wetlands; PSII

Introduction

Although occupying only approximately 4–6% of land area, wetland ecosystems are the most important "carbon sink" or "carbon source" for terrestrial ecosystems. Wetland ecosystems are rich in animal and plant resources and have an important ecological value (Gorham 1991; Wang *et al.* 2009; Andreetta *et al.* 2016). The Momoge National Reserve wetland in Jinlin Province, it is the largest concentrated marsh wetland in China, and was added to the List of China important wetlands in 2002 (He *et al.* 2001; Xiao *et al.* 2015). The wetland of Jilin Province plays an important role in regulating the local climate by controlling the emission of greenhouse gases and carbon fixation, which has important ecological values. However, the

wetland ecosystem has been impacted due to large-scale reclamation. In recent decades, the wetland area of the Jilin Province has been greatly reduced because of overexploitation. Many problems, such as soil erosion, the reduction of biodiversity in wetlands, and environmental pollution, are becoming increasingly serious (Liu *et al.* 2014; Liu *et al.* 2016).

Wetland degradation is mainly manifested in the decrease of water content, which directly leads to the mineralization of soil organic carbon and the increase of greenhouse gas emissions in wetlands, ultimately contributing to global climate change. Water is an important limiting factor affecting the biodiversity in wetland ecosystems. The main performance of wetland degradation is the decrease of water content. This factor directly leads to

the mineralization of wetland soil organic carbon, the increase in wet chamber gas emissions, and the global climate change. Water is also one of the important factors affecting the biodiversity of wetland ecosystem (Liu et al. 2009; 2014; Bai et al. 2010). Previous studies have examined the species composition and diversity in wetlands (Song et al. 2005; Sui et al. 2016), including the diversity of soil bacteria, fungi, and soil enzymes (Sui et al. 2017), indicating that species composition changes under different water gradients. Water is an important limiting growth factor affecting the physiological function of plants. Different plants have different demands for water. Drought or excessive water will restrict the physiological function of plants (Hou et al. 2011; Wu et al. 2019). However, due to the long-term or seasonal flooding conditions, wetland plants have formed a unique mechanism of physiological and ecological adaptation. At present, studies on the growth of wetland plants such as *Deyeuxia angustifolia* (Wu et al. 2019) under different water gradients have been reported. There are few studies on the photosynthetic physiological adaptability of the dominant plants in different degraded wetlands. Since *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia* are the typical dominant species in the wetland, it is important to understand its mechanisms of physiological adaptation under different water conditions. The photosynthetic capacity of plants is the basis of plant growth, especially the function of photosystem II (PSII), which has a great significance in the utilization of light energy. PSII is also sensitive to environmental factors. For example, PSII is often reduced under adverse conditions and even induces photoinhibition (Mittler 2002).

In this study, *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia* were selected as typical wetland dominant plants in Jilin Province. The PSII function changes of three dominant plant leaves in degraded wetland were studied by using chlorophyll fluorescence dynamics. The adaptation mechanism of the main wetland vegetation to the degraded wetland environment was revealed through photosynthetic function, in order to provide some information for photosynthetic function and to provide basic information for further research on the dominant plant in the wetland of Jilin Province.

Materials and Methods

Test site survey and soil sample collections

The experimental site is located in Momoge National Reserve of Jilin Province (45° 42' 25" N, 123° 27' 0" E), the experimental site belongs to the temperate humid semi humid monsoon climate, with an altitude of 60–70 m and an annual average rainfall of 500–600 mm, and it is mainly concentrated in summer and autumn, with an annual average temperature of 2.3°C, frost free period of about 125 days (He et al. 2001; Wang et al. 2017), the wetland sampling area is located in the core wet land area of the

reserve, and the dominant wetland plants are *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia*.

Soil samples were collected and the determination of water content in wetlands with degraded wetlands: Five soil samples were collected along an “S” shape path and were mixed together. The sampling depth was approximately 0–20 cm, and the sampling depth in the marshes excludes the water depth. The soil samples were packed in plastic sealed bags, and the soil moisture content was measured by oven drying in the laboratory. Additionally, five strains of *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia* with relatively consistent growth were selected in each degraded wetland to determine their PSII photochemical activity. Five repetitions were conducted for each treatment.

Determination methods

The gas exchange parameters: Net photosynthetic rate (p_n), stomatal conductance (G_s), in intercellular CO_2 concentration (C_i) and transpiration rate (T_r) were measured at 8:00–10:00 am, and using Licor-6400 portable photosynthesis instrument (Licor-6400 Portable Photosynthesis System, Licor, USA). Keep portable at the 65% relative humidity, $400 \mu mol m^{-2} s^{-1}$ and $1000 \pm 50 \mu mol m^{-2} s^{-1}$.

Determination of the chlorophyll fluorescence curve (OJIP): Dark adaptation of *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia* leaves collected from different degraded wetlands was applied for 25–35 min by a dark adaptation. The OJIP curves were determined using a plant efficiency analyzer (Handy-PEA), which was induced by a pulsed red light of $3,000 \mu mol \cdot m^{-2} \cdot s^{-1}$. The average value of fluorescence intensity from the five repeated measurements at each time point was used to draw the OJIP curve, and the abscissa of the curve was expressed in the logarithmic form. The relative variable fluorescence of each point at the O–P, O–J and the O–K standardization was calculated as by the methods of Zhang et al. (2012; 2013a), and using the JIP-test to calculate the maximum photochemical efficiency (F_v/F_m) of PSII and the photosynthetic performance index (PI_{ABS}) based on light energy absorption (Hendrickson et al. 2004).

Determination of the chlorophyll fluorescence photoresponse curve: The photoresponse curve of chlorophyll fluorescence in *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia* leaves under different degraded wetlands was measured using a portable pulse modulation fluorometer (FMS-2, Hansatech, UK). The maximum fluorescence (F_m) and the initial fluorescence (F_o) were determined after the leaf samples were dark adapted for 25–35 min using a dark adaptation clip. Then, the fluorescence parameters of the light adaptation treated leaves were determined, including the maximum fluorescence (F_m'), the minimum fluorescence (F_o'), and the steady-state fluorescence (F_s). Actual photochemical efficiency (Φ_{PSII}) and the electron transport rate (ETR) under different light

intensities were calculated using the following formulas: $\Phi_{PSII} = (F_m/F_s)/F_m'$ and $ETR = 0.5 \times 0.85 \times \Phi_{PSII} \times PFD$, respectively, and the photoresponse curve of Φ_{PSII} and ETR were plotted.

Determination of the parameters of light energy distribution in the PSII reaction center: *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia* leaves collected from different degraded wetlands were dark adapted for 30 min using a dark adaptation. Then, a portable pulse modulated fluorometer FMS-2 (Hansatch Company, UK) was used to determine the direction of absorbed light energy in the PSII reaction center, such as the quantum yield for photochemical reaction (Φ_{PSII}), the quantum yield relying on the proton gradient on both sides of the thylakoid membrane and the lutein cycle (Φ_{NPQ}), the basic fluorescence quantum yield and the quantum yield of heat dissipation (Φ_{ID}), and the quantum yield of heat dissipation in deactivated PSII reaction centers (Φ_{NF}) described by Hendrickson *et al.* (2004).

Data processing and statistical analysis

The data in each graph is presented as the average value $\pm$ standard error (SE) of five replicates. Statistical analyses were conducted using Excel and SPSS (25.0), and the difference between different data groups was compared using a one-way analysis of variance (one-way ANOVA) and least significant difference test (LSD).

Results

The gas exchange parameters of three dominant plants in degraded wetland

The P_n , G_s , T_r and C_i of three dominant species plant under the background conditions of wetland degradation (Fig. 1A–D). The leaves of *C. pseudocuraica* and *D. angustifolia* had higher P_n , G_s and T_r than *C. lasiocarpa* ($P < 0.05$), the intercellular CO_2 concentration (C_i) in the leaves of *C. pseudocuraica* and *D. angustifolia* were significantly lower than that of *C. lasiocarpa* ($P < 0.05$). But these differences in *C. pseudocuraica* and *D. angustifolia* were not significant. ($P < 0.05$)

OJIP curve of three dominant plants in degraded wetland

The OJIP curves of *C. pseudocuraica* and *D. angustifolia* were similar (Fig. 2). Compared with *C. lasiocarpa*, the relative fluorescence intensity (RFI) F_o at point O in the leaves of *C. pseudocuraica* and *D. angustifolia* decreased significantly. The RFI F_m at point P exhibited a significantly increasing trend, but the changes of RFI at point J under degraded wetland were not significant. On the other hand, the RFI at point I increased distinctively, but the range of increase was significantly smaller than that at point P.

F_o , F_m , F_v/F_m and PI_{ABS} of three dominant plants in degraded wetland

The results of the quantitative analyses on F_o and F_m (Fig. 3A–B) show that compared with plants collected from *C. lasiocarpa*, the F_o in the leaves of plants collected from *C. pseudocuraica* and *D. angustifolia* decreased by 31.36% ($P < 0.01$) and 30.25% ($P < 0.01$), respectively, and both differences were not significant; but F_m increased by 9.35% ($P < 0.05$) and 10.71% ($P > 0.05$), respectively, and these differences were not significant ($P < 0.05$). The F_v/F_m of *C. lasiocarpa* was lower than that in leaves from *C. pseudocuraica* and *D. angustifolia* by 16.72% ($P < 0.05$) and 18.98% ($P < 0.05$), respectively; the PI_{ABS} in *C. lasiocarpa* was lower by 30.07% ($P > 0.05$) and 41.94% ($P > 0.05$), respectively (Fig. 3C–D). The F_v/F_m and PI_{ABS} in *C. pseudocuraica* and *D. angustifolia* were both not significant.

Standardized O–P, O–J, and O–K curves of three dominant plants in degraded wetland

There were significant differences in the RFI of point J and I (V_J and V_I) were shown on the standard O–P curve, the RFI of point K (V_K) on the standard O curve, and the RFI of point L (V_L) on the standard O–K curve (Fig. 4C–D). The V_J , V_K , and V_L of leaves in *C. pseudocuraica* and *D. angustifolia* were significantly lower than those in *C. lasiocarpa* based on ΔV_{O-P} , ΔV_{O-J} , and ΔV_{O-K} .

Relative variable fluorescence at point J, K, and L in three dominant plants in degraded wetland

Quantitative analyses of the relative variable fluorescence on each characteristic point (V_J , V_K , and V_L) of the standardized O–P, O–J, and O–K curves were conducted (Fig. 5). Compared with *C. lasiocarpa*, the decrease in water content in the wetland caused the reduction of V_J , V_K , and V_L in *D. angustifolia* leaves, but the degree of reduction for each point was distinctly different. The degrees of reduction of V_J , V_K , and V_L in the leaves from *D. angustifolia* were slightly higher than that from *C. pseudocuraica*, but these differences were not significant. V_J and V_K were different between *C. pseudocuraica* and *D. angustifolia*, but this difference was not significant. The difference of V_J and V_K in the leaves from was significantly lower than *C. lasiocarpa*. In addition, the V_J in *C. pseudocuraica* and *D. angustifolia* was lower than that in *C. lasiocarpa* by 9.15% ($P < 0.05$) and 12.42% ($P < 0.05$), respectively, and both of these differences were significant.

Chlorophyll fluorescence parameters in three dominant plant leaves under the background of degraded wetland

The Φ_{PSII} and ETR of the three dominant plants in the context of degraded wetland are significantly different (Fig. 6A–B). However, with the increase of light intensity, the reduction of Φ_{PSII} and the increase of ETR in *C. lasiocarpa* were significantly lower than those in *C.*

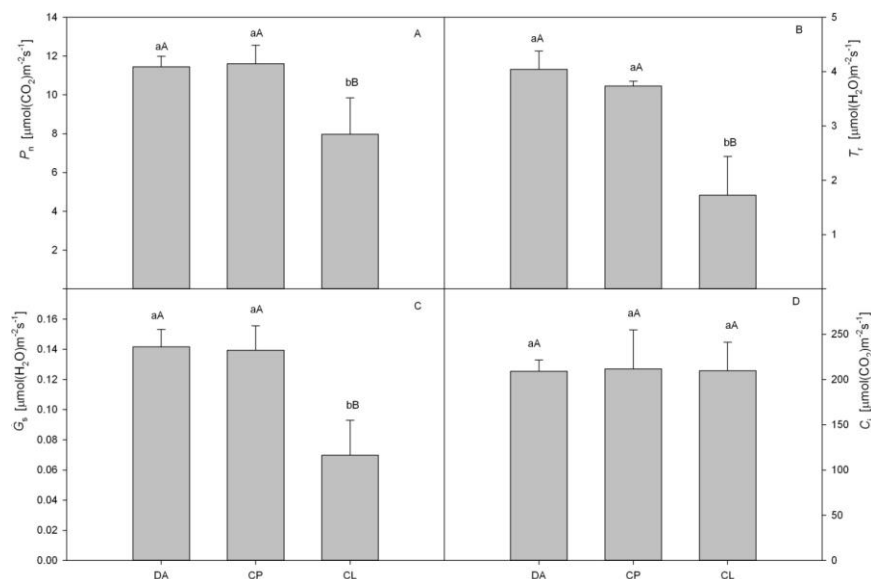


Fig. 1: The gas exchange parameters of three dominant plants in Degraded Wetland

Note: The net photosynthetic rate (A), transpiration rate (B), stomatal conductance (C) and the intercellular CO_2 concentration (D) in leaves of three dominant plants in Degraded Wetland. Data in the figure are mean $\pm$ SE, values followed by different small letters mean significant difference ($p < 0.05$). DA: *D. angustifolia*; CP: *C. pseudocuraica*; CL: *C. lasiocarpa*

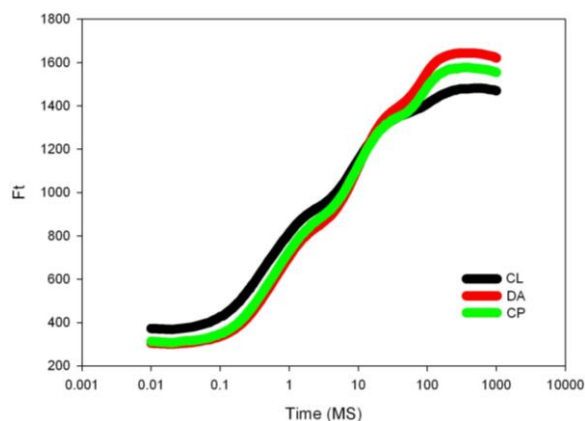


Fig. 2: OJIP curve of three dominant plants in Degraded Wetland

Note: DA: *D. angustifolia*; CP: *C. pseudocuraica*; CL: *C. lasiocarpa*

pseudocuraica and *D. angustifolia*. Φ_{PSII} and ETR in the leaves of *C. pseudocuraica* were slightly lower than those in *D. angustifolia*, but the differences were limited.

Energy distribution parameters of the PSII in the leaves of three dominant species plant under the background conditions of wetland degradation on PSII

The energy distribution parameters of *D. angustifolia* leaves under different water gradients the leaves of three dominant plant species under the background conditions of wetland degradation were different (Fig. 7). After the water content decreased under the background conditions of wetland degradation, the Y_{PSII}

in leaves from *C. pseudocuraica* and *D. angustifolia* increased by 20.49 and 20.59%, respectively, compared with *C. lasiocarpa*; the change in Y_{NPQ} was not significant and both $Y_{\text{f,D}}$ and Y_{NF} decreased to different degrees.

Discussion

Plant growth is inhibited by long-term flooding mainly due to the decline of root activity under the low oxygen environment, resulting in a slower respiration rate or even anaerobic respiration (Tariq et al. 2017; Xia et al. 2017). Long-term flooding can also affect the photosynthetic capacity of plants, resulting in decrease of chlorophyll content, closure of stomata, and decline of in photosynthetic capacity (Liang et al. 2003; Sharma et al. 2015; Xia et al. 2017). After the plants are flooded, the subcellular structures in the leaf cells are damaged, and the activity of both photosynthetic enzymes and the PSII reaction center are reduced (Gosling and Arnell 2016; Guo et al. 2018). However, aquatic plants have a very strong adaptability to flooding conditions due to their unique root structure. The key to the survival of these aquatic plants depends on changes in physiological adaptability after seasonal flooding and water receding, especially the adaptability of typical wetland plants to different water gradients after wetland degradation. The decrease in water content will inhibit the growth of plants and affect the photosynthetic capacity of plants, resulting in the decrease of chlorophyll content, stomatal closure and photosynthetic capacity of plants (Reddy et al. 2004; Guo et al. 2018). Photosynthesis is the basis of organic matter accumulation, growth and

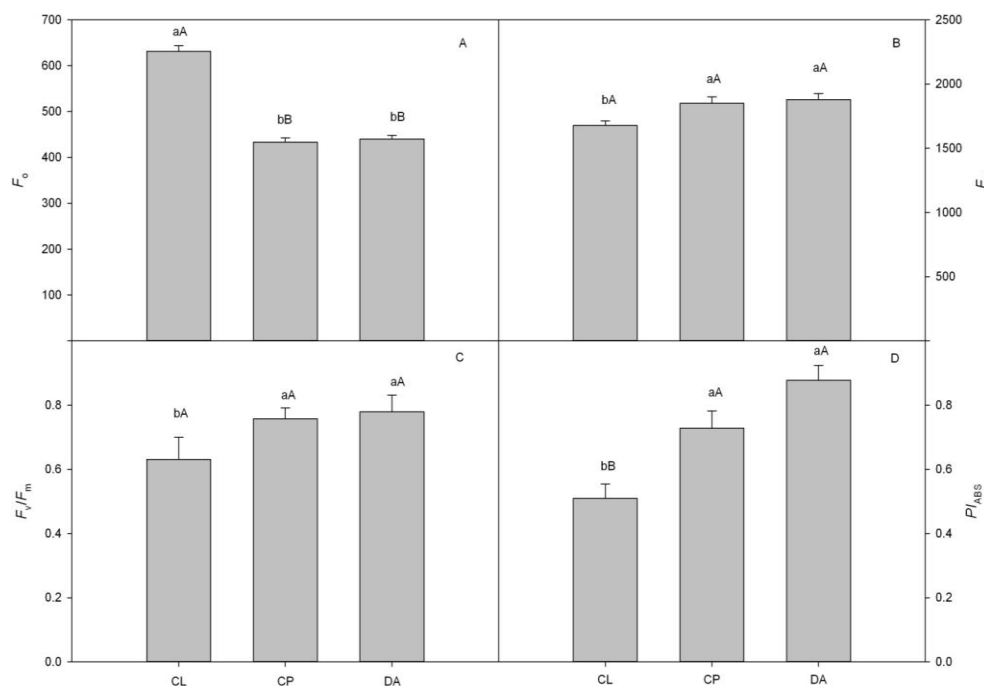


Fig. 3: F_0 , F_m , F_v/F_m and PI_{ABS} of three dominant plants in Degraded Wetland

Note: The initial fluorescence (A), the maximum fluorescence (B), the maximum photochemical efficiency (C) the photosynthetic performance index (D) in leaves of three dominant plants in Degraded Wetland. Data in the figure are mean $\pm$ SE, values followed by different small letters mean significant difference ($p < 0.05$). DA: *D. angustifolia*; CP: *C. pseudocuraica*; CL: *C. lasiocarpa*

development of plants, which is affected by physiological characteristics of plants and environmental factors. Soil moisture is an important factor affecting the photosynthetic process. The results of this experiment showed that the P_n , G_s and T_r of *C. lasiocarpa* and *C. microphylla* are significantly lower than *C. pseudocuraica* and *D. angustifolia*, the results showed that the photosynthetic carbon assimilation ability of *C. pseudocuraica* and *D. angustifolia* was stronger than *C. lasiocarpa*. Although the lower G_s of *Carex lasiocarpa* could effectively reduce the water loss caused by transpiration, it also increased the diffusion resistance of CO_2 to the leaves, resulting in lower photosynthetic energy (Fig. 1). The ultrastructural damage, photosynthetic enzyme activity and PSII reaction center activity of leaf cells decreased after water deficiency (Liang *et al.* 2003; Murata *et al.* 2007; Hund *et al.* 2009; Li *et al.* 2010). However, due to the unique structure of the root system of aquatic plants, it has a strong adaptability to water. What changes will happen to the physiological adaptability of aquatic plants to the degradation wetland after the reduction of water content caused by environmental changes? In particular, whether the typical wetland plants have the ability to adapt to water loss after wetland degradation is the key to determine whether they can become adapted species.

Plant photosynthetic capacity is one of the most sensitive physiological processes to the environment, and chlorophyll fluorescence technology is an important method to study the photosynthetic mechanism of plants, especially

the function of PSII (Farooq *et al.* 2009; 2015; Zhang *et al.* 2016). In this study, the function of PSII in *C. lasiocarpa*, *C. pseudocuraica* and *D. angustifolia* leaves, typical species in the degraded wetland of Jilin province, was studied using fast chlorophyll fluorescence kinetics (Zhang *et al.* 2016). The results showed that F_v/F_m and PI_{ABS} of leaves of *C. pseudocuraica* and *D. angustifolia* increased to different degrees compared to that in *C. lasiocarpa* under the background conditions of wetland degradation. Both the F_v/F_m and PI_{ABS} are important indexes reflecting the photochemical activity of PSII in plants, so the results also reveal that the photochemical activity of PSII of *C. pseudocuraica* and *D. angustifolia* increased compared with that in *C. lasiocarpa*, which may be due to lower soil water content or a sufficient O_2 supply obtained in the roots of *D. angustifolia* under the alternation of flood and non-flood conditions (Fig. 3). In addition, both the F_v/F_m and PI_{ABS} of leaves from *C. pseudocuraica* and *D. angustifolia* were slightly higher than those from *C. pseudocuraica*, which further verified that when soil oxygen supply increases, the photosynthetic function of the leaves of dominant species are enhanced.

In order to further analyze the causes of the different PSII photochemical activity of the leaves of three dominant species plant under the background conditions of wetland degradation, the OJIP curve in three dominant species plant leaves was standardized, and the change of the variable fluorescence of each characteristic point

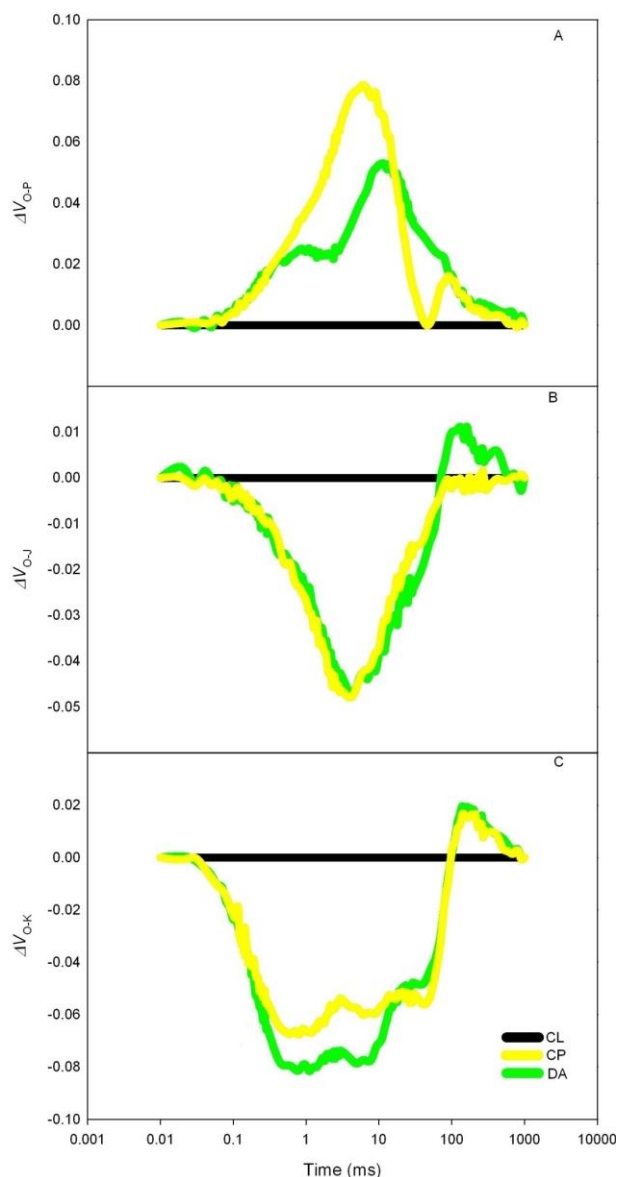


Fig. 4: Standardized O-P, O-J, and O-K curves of three dominant plants in Degraded Wetland

Note: The original OJIP curve was normalized by O-P (A); the original OJIP curve was normalized by O-J (B); the original OJIP curve was normalized by O-K. DA: *D. angustifolia*; CP: *C. pseudocuraica*; CL: *C. lasiocarpa*

on the standardized curves was analyzed. The results showed that the V_J , V_K , and V_L at each point of the standardized O-P, O-J, and O-K curves in *C. pseudocuraica* and *D. angustifolia* were significantly lower when compared with that in *C. lasiocarpa*. The V_J at point J (2 ms) of the standardized O-P curve reflects the accumulation of Q_A , hence the enhancement of V_J , indicating that the electron transfer of Q_A to Q_B on the PSII receptor side was blocked (Santos and Rey 2006; Zhang et al. 2013a; 2013b; Zhang et al. 2016). The increase in the relative variable fluorescence, V_K , at point K (0.3 ms) of the

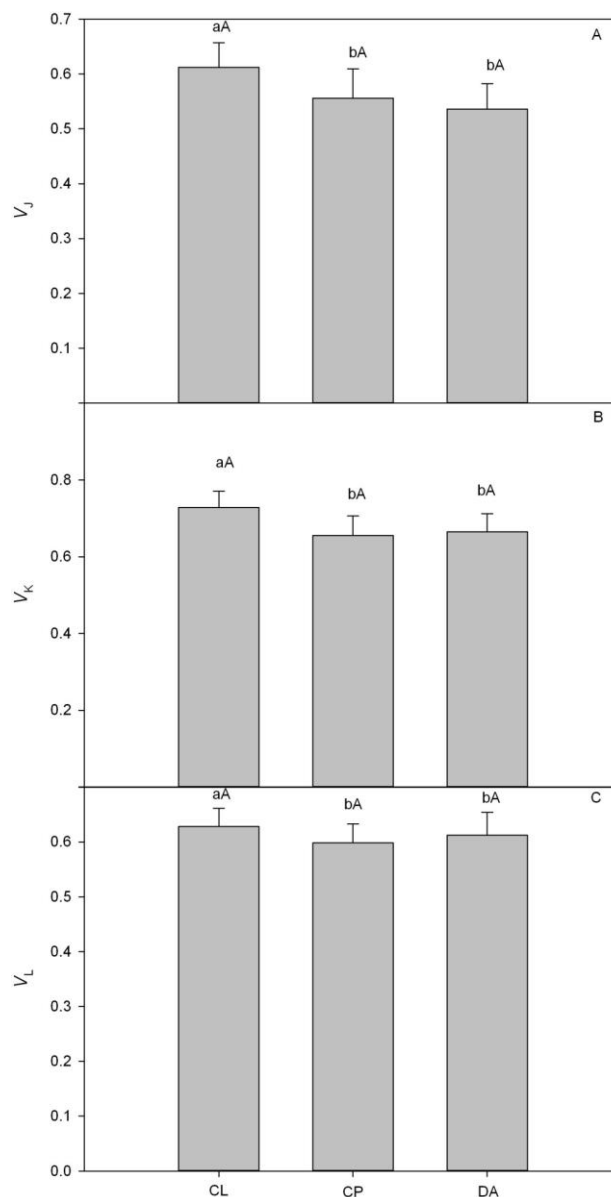


Fig. 5: Relative variable fluorescence at point J, K, and L in three dominant plants in Degraded Wetland

Note: the standardized O-P curves (A); the standardized O-J curves (B); the standardized O-K curves. DA: *D. angustifolia*; CP: *C. pseudocuraica*; CL: *C. lasiocarpa*. Data in the figure are mean $\pm$ SE, values followed by different small letters mean significant difference ($p < 0.05$)

standardized O-J curve is considered to be a specific indicator of injury to the activity of OEC on the PSII electron donor side (Santos and Rey 2006; Zhang et al. 2012; Zhang et al. 2013b; Chen et al. 2017), while the increase of the relative variable fluorescence V_L at point L (0.15 ms) of the standardized O-K curve is considered to be an important indicator for the damage of the thylakoid membrane. Hence, after the decrease of soil moisture in *C. pseudocuraica* and *D. angustifolia*, the electron transfer rate of *C. pseudocuraica* and *D. angustifolia* leaves on the PSII

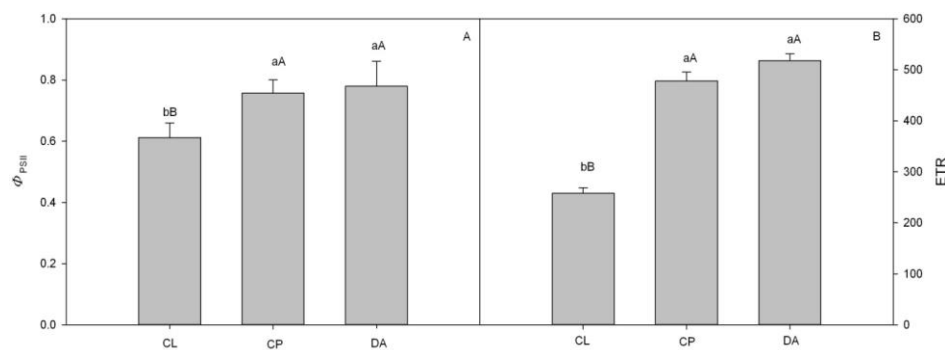


Fig. 6: Chlorophyll fluorescence parameters in three dominant plant leaves under the background of degraded wetland.

Note: Actual photochemical efficiency (A); the electron transport rate (B); DA: *D. angustifolia*; CP: *C. pseudocuraica*; CL: *C. lasiocarpa*. Data in the figure are mean $\pm$ SE, values followed by different small letters mean significant difference ($p < 0.05$)

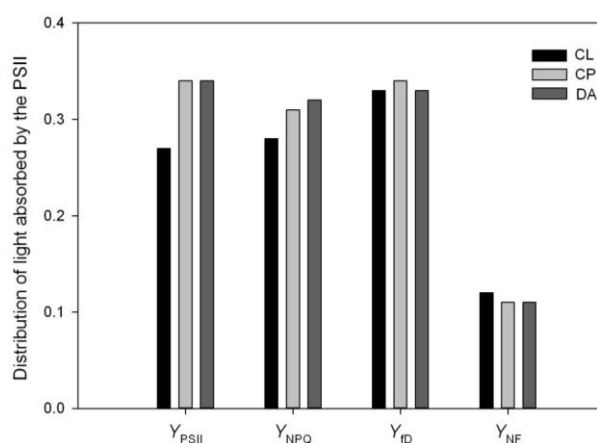


Fig. 7: Energy distribution parameters of the PSII reaction center in the leaves of three dominant species plant under the background conditions of wetland degradation on PSII

Note: the quantum yield for photochemical reaction (A); the thylakoid membrane and the lutein cycle (B); the basic fluorescence quantum yield and the quantum yield of heat dissipation (C); the quantum yield of heat dissipation in deactivated PSII reaction centers (D). DA: *D. angustifolia*; CP: *C. pseudocuraica*; CL: *C. lasiocarpa*

receptor side and the OEC activity on the donor side both increased to varying degrees compared with those in *C. lasiocarpa*, and the stability of the thylakoid membrane in *C. pseudocuraica* and *D. angustifolia* leaves also improved (Fig. 4–5). Thus, this relates to the increase in photochemical activity in PSII. The enhancement of PSII function in *C. pseudocuraica* and *D. angustifolia* leaves is very important for maintaining normal photosynthetic carbon assimilation in leaves and for promoting the growth of *C. pseudocuraica* and *D. angustifolia*. This is consistent with the results from a study conducted by Wang *et al* (2008) in which the biomass of a *D. angustifolia* community without perennial ponding was higher than that of a community with perennial ponding.

Chlorophyll fluorescence parameters Φ_{PSII} and ETR can be used to analyze the utilization of light intensity of plants (Yang *et al.* 2005; Gameiro *et al.* 2016). The decrease of Φ_{PSII} and the increase of ETR of *C. lasiocarpa* leaves are

significantly lower than those of *C. pseudocuraica* and *D. angustifolia* leaves (Fig. 6), while the difference of Φ_{PSII} and ETR of *C. pseudocuraica* is slightly lower than that of *D. angustifolia* leaves (Fig. 6). This indicates that *C. pseudocuraica* and *D. angustifolia* were better able to use light energy, especially high light intensity, which was obviously better than *C. lasiocarpa*. In addition, the study on the energy absorption in the PSII showed that the Y_{PSII} of leaves from *C. pseudocuraica* and *D. angustifolia* significantly increased after the water content in the soil decreased, indicating that the proportion of light energy absorbed for photochemical reactions in leaves from *C. pseudocuraica* and *D. angustifolia* is higher than that *C. lasiocarpa*. This has a positive effect on maintaining the normal photosynthetic electron transfer and on ensuring the supply of assimilate (NADPH and ATP). The difference in Y_{NPQ} of leaves from *C. pseudocuraica* and *D. angustifolia* was not significant, but both Y_{ID} and Y_{NF} decreased to some degree. This reveals that when water content in the soil decreases, the proportion of energy dissipation excitation energy in the form of ineffective heat decreases, and the energy proportion allocated to the inactive reaction center decreases, which is important for maintaining the energy supply for normal photosynthetic processes in leaves.

Conclusion

Compared to *C. lasiocarpa*, the function of PSII in leaves from *C. pseudocuraica* and *D. angustifolia* increased to varying degrees after decrease in soil moisture of wetlands degraded wetland. This is mainly manifested in the following points: the increase in photochemical efficiency of PSII; the improvement of both the activity of OEC on the donor side of PSII and the electron transfer capacity on the receptor side of PSII; the enhancement of the ability to use light energy, especially under intense light conditions; and the optimization of light energy utilization and distribution. This may be one of the most important reasons that had led to *C. pseudocuraica* and *D. angustifolia* becoming a dominant species in degraded wetland. However, a

relatively small difference in PSII function between leaves from *C. pseudocuraica* and *D. angustifolia* was observed.

Author Contributions

DJ and XN planned the experiments, SZ, HN and BA interpreted the results, DJ, XN and XL made the write up and BA statistically analyzed the data and made illustrations

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