Effect of Elevated CO₂ Concentration On Four *Populus* by the Fast Fluorescence Rise OJIP

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Abstract Increased atmospheric carbon dioxide (CO₂) can influence the stability of ecosystems in the world. The chlorophyll fluorescence technique was considered as an effective tool to evaluate the photosynthetic levels on many plant species. In this study, we analyzed the state of PSII on four kinds of populus (*Populus* L.) (*populus* X, *Populus deltoides* × *cathayana*, *Populus alba* 'Berdinensis' L, *Populus euramericana* 'N3016' × *Populus ussuriensis*) under high CO₂ condition. The results show that the PSII performance was negatively influenced by CO₂ stress. High CO₂ stress resulted in down-regulation of *Fm*, *φPo* (= *Fv*/*Fm*), *ψEo*, *φEo* and *Ptotal* in four kinds of *populus*. And a significant decrease in the P-step level of the fluorescence transients OJIP curves of four *populus* species after 7 days of treatment was observed. Therefore, a fast decrease of the P-step level indicated there was main change to fluorescence transients. These results indicated that changes of PSII attribute to the degradation of antenna pigment and inhibition of the electron transport at the acceptor side of PSII.

Keywords *Populus* L., Atmospheric carbon dioxide (CO₂), Photosynthetic performance, OJIP

Background

Environmental changes for emissions of greenhouse gasses have influenced the stability of ecosystems in the world (IPCC, 2007). Accordingly, the increased atmospheric CO₂ concentration (EC) has become the most important environmental issues in the world. Especially, human activities lead to increased CO₂ concentration in the atmosphere, which is expected to reach 700 μL/L by the middle of the next century (Amthor, 2010; Griffin et al., 2001; Long et al., 2004; Peters and Hertwich, 2008). Various researches showed EC can effect the development, growth and yield of plant. In addition, EC can increase photosynthetic rates. In the result, high photosynthetic rates will improve growth of plants. For these reasons, there is a large of reports on the physiological responses of plants to EC, however, little studies have given account of the response of woody plants to EC. In this study, here, we tested the effects of EC on the growth and photosynthetic characteristics of four *populus* (*Populus* L.).

Poplars (*Populus* L.) are most widespread and fastest growing tree species, and their wood can be used for construction, paper, and fossil fuels. Poplars are known to be sensitive to various environmental stresses (Cui et al., 1999; Jiang et al., 2007). To date, the effects of EC on physiology and growth of poplars have been studied. For instance, EC treatments did not bring changes in structure of wood of birch (Kostiainen et al., 2008). EC also reduced tree height and photosynthetic pigment contents of *Populus alba* × *glandulosa*. Generally, the photosynthetic ability was reported to a reliable indirect indicator of tree performances under different environmental stress. However, there is few knowledge on photosynthetic responses on different *Populus* species to EC (Verhoeven et al., 1999; Jiang et al., 2002). Several past studies have found chlorophyll a fluorescence technique to be suitable as a stress indicator and for monitoring physiological changes in the plant. The chlorophyll a fluorescence OJIP transient (OJIP transient) technique was suitable.

Due to simple, non-destructive, and rapid characteristics, this technique has been used to evaluate the

photosynthetic levels on many plant species (Strasser et al., 2000; Strasser et al., 2004; Zushi et al., 2012; Guo and Tan, 2015). The OJIP transient is defined by the O, J, I, and P steps, which correspond to the redox states of the photosystem (PS II and PS I) (Strasser et al., 2000; Strasser et al., 2004). Indeed, several studies have been conducted on OJIP transients in salt-stressed plants (Guo and Tan, 2015). For example, in salt-stressed wheat leaves, OJIP transients and the calculated JIP parameters can be used as sensitive methods to assess the stress level and to identify the action sites of salt stress (Mehta et al., 2010). It has also been shown that in salt-stressed canola (*Brassica napus*) leaves (100 mM and 200 mM NaCl), salt stress does not significantly affect the values of JIP parameters related to the electron donor site in PSII; However, the values of the JIP parameters that are related to the electron acceptor site significantly decrease with an increasing concentration of salt (Jafarinia and Shariati, 2012).

In our study, we have examined photosynthetic responses of four *Populus* spp. species to EC by chlorophyll a fluorescence OJIP transient (OJIP transient) technique. Due to simple, non-destructive, and rapid characteristics, this technique has been used to evaluate the photosynthetic levels on many plant species. Indeed, this method can provides valuable information to the redox states of the photosystem (PS II and PS I) (Šesták et al., 2001; Force et al., 2003; Jiang et al., 2003; Heerden et al., 2004; Albert et al., 2005; Schansker et al., 2005; An, 2006; Il k et al., 2006; Strauss et al., 2007; T áth et al., 2007; Chen et al., 2008; Strasserf et al., 2008; Yordanov et al., 2008). PS II is very sensitive to environmental stresses (Verhoeven et al., 1999; Jiang et al., 2002). However, a study of comparing influences of EC on PSII behaviors of woody species is still lack. Therefore, a detailed comparison of high CO₂-induced changes in PSII photochemistry in different *Populus* spp. species was carried out by OJIP technique. In this study, we analyzed the transient fluorescence using JIP-test on four *Populus* species (*populus* X, *Populus deltoides* × *cathayana*, *Populus alba* 'Berdinensis' L, *Populus euramericana* 'N3016' × *Populus ussuriensis*) under atmospheric CO₂ (1500 ± 50 μmol/mol). Our objectives were to determine that whether different *Populus* species vary in their PS II traits under EC.

1 Results

1.1 OJIP curves on four *populus*

In OJIP curves of leaves, each step exhibited a different response to EC for four *populus* species (Figure 1A-D). All O-J-I-P transients were normalized at the O step and P step. Effects of EC on JIP parameter values were different, and specific changes were observed in some *populus* species. For example, relative fluorescence intensity was decreased for *populus* X at the 7th day after treatment, especially, the fluorescence intensity from I- to P- step was inhibited (Figure 1A). Conversely, relative fluorescence intensity of *Populus deltoides* × *cathayana* was increased and relative fluorescence intensity was also increased from J- to I- step (Figure 1B). However, relative fluorescence intensity from J- to I- step of *Populus alba* 'Berdinensis' L was similar between control and treatment (Figure 1C). For *Populus euramericana* 'N3016' × *Populus ussuriensis*, an increase in relative fluorescence intensity was also observed from I- to P- step (Figure 1D).

1.2 Fluorescence parameters on four *populus*

The values (treated and control) of the JIP test parameters are shown in Table 1 and Table 2. No significant changes were observed in the minimum fluorescence (F_o), fluorescence at the J-step (F_j) and fluorescence at the I-step (F_i). In contrast, drastic decreases in F maximum fluorescence (F_m) values of four *populus* species were recorded after 7 days of CO₂ treatment (Table 2). Similarly, all *populus* species showed significant decrease in maximum quantum yield of PSII primary photochemistry (ϕPo), the efficiency on the energy of a trapped exciton converting into electron transport beyond QA- (ψEo), the quantum yield of electron transport beyond QA (ϕEo) and total performance index per absorption basis (P_{total}) after treatment. Especially, P_{total} value sharply decreased after treatment. On the other hand, the values of relative variable fluorescence at the J-step (V_j) and relative variable fluorescence at the I-step (V_i) on treated-plants were higher than those of controls. The value in ABS/RC of treated plants is higher than those of control plants. However, effects of EC on *Populus deltoides* × *cathayana* did not show specific changes in CO₂-treated plants compared control plants (Table 2).

Figure 1 The relative fluorescence transients in fully dark-adapted *populus X* leaves (A), *Populus deltoides* × *cathayana* leaves (B), *Populus alba* 'Berdinensis' L leaves (C) and *Populus euramericana* 'N3016' × *Populus ussuriensis* leaves (D) under CO₂ stress and the control condition at 7 days

2 Discussion

In this study, the shapes of chlorophyll a fluorescence transient (O-J-I-P) were markedly different in four *populus* species after high CO₂ treatment, however the values of F_v/F_m showed similar decreasing tendency (Table 2). Thus, there is the heterogeneous behavior of PSII in *populus* leaves different from F_v/F_m . Generally, the level of photochemical reaction can be evaluated according to the chlorophyll fluorescence intensity. And F_v/F_m can also be used to describe the trapping efficiency of the absorbed light, which can reduce primary quinone electron acceptor of PSII (Q_A) (And and Weis, 2003). Therefore, the different fluorescence transients of leaves under high CO₂ levels indicated that the photochemical reactions were different for different *populus* species, although there were similar decreasing F_v/F_m (reflecting trapping efficiencies of the absorbed light). In contrast, previous studies showed the F_v/F_m ratio reflects the photochemical efficiency of PSII (Rachoski et al., 2015). Various environmental stress can lead to inhibition of photosynthetic efficiency, accordingly, affecting state of the photosynthetic apparatus.

For O-J-I-P, point O can represent the fluorescence of PS II action center, if all of the electron acceptor (Q_A , A_B , PQ, etc.) are fully open in the maximum oxidation state. The fluorescence intensity of point O is connected with the content of the antenna pigment and the activity of action center. Point J reflects the rate of reduction of Q_A , which is connected with reaction centre pigments, light-harvesting pigment and the state of Q_A and Q_B . If the electrons transfer from Q_A to Q_B is restricted, the value of point J will rise (Ainsworth and Long, 2005). Here, higher J value in the leaves was observed. In addition, point I reflects the heterogeneity of PQ, the electron

acceptor state in point I mainly is related to Q_A^- and Q_B^{2-} . Furthermore, the structure and function of PS II complexes and the size of the PQ library is attributed to appearing time of point P. In this study, high CO_2 level caused a significant decrease in the P-step level of the fluorescence transients OJIP curves of four *populus* species after 7 days of treatment. Therefore, a fast decrease of the P-step level indicated that there was main change to fluorescence transients. Generally, the “P” level was connected with the process of the electron transportation from Q_B to PQ, and it can mark concentrations of both Q_A^- Q_B^{2-} and PQH (Stirbet et al., 1998; Hill et al., 2004). Additionally, no significant changes in F_o , F_j and F_i of different *populus* species were observed after high CO_2 treatment. Generally, high CO_2 stress can lead to decrease of F_m , which reflects maximum fluorescence intensity at the P-step (Li et al., 2005). Therefore, this result suggested that the F_m may be a good marker of PSII vitality under high CO_2 stress.

The PSII switches from the process of converting light energy into biochemical energy storage to the energy conversion process that transforms absorbed light energy into heat dissipation (Thach et al., 2007). One of PI_{total} is used to analyze the response of the plant's PSII. Accordingly, it is sensitive to changes in either antenna properties, trapping efficiency or electron transport beyond Q_A (Oukarroum et al., 2007). In this study, we found that PSII performance can be represented using PI_{total} . In general, PI_{total} is also influenced by changes in antenna, RC, electron transport and end-acceptor reduction dependent parameters. Thus, PI_{total} integrates the response of RC/ABS, $TR_o/ABS(=F_v/F_m)$, $ET_o/TR_o(=[1-V_j])$ and $RE_o/ET_o(=[1-V_i]/[1-V_j])$.

Table 1 Formulae and explanation the technical data of the OJIP curves and the selected JIP-test parameters used in this study

Measured parameters from the chlorophyll- α fluorescence transient	
F_t	Fluorescence intensity at time measured after onset of actinic illumination
$F_o = F_{20\mu s}$	Minimum reliable fluorescence intensity at 20 μs
F_l	Fluorescence intensity at the L-step (100 μs)
F_k	Fluorescence at the K-step (300 μs)
F_j	Fluorescence at the J-step (2 ms)
F_i	Fluorescence at the I-step (30 ms)
$F_p = F_m$	Maximum fluorescence intensity at the P-step
Derived parameters	
Selected OJIP-test parameters	
$V_j = (F_{2ms} - F_o)/(F_m - F_o)$	Relative variable fluorescence at the J-step
$V_i = (F_{30ms} - F_o)/(F_m - F_o)$	Relative variable fluorescence at the I-step
$Mo = 4 \times (F_{300s} - F_o)/(F_m - F_o)$	Approximated initial slope per ms of the fluorescence transient
$ABS/RC = [Mo/V_j] \times [1/(F_v/F_m)]$	Measure of the average total absorbance per active PSII RC
Quantum yields	
$\phi Po = TR_o/ABS = (F_m - F_o)/F_m = F_v/F_m$	Maximum quantum yield of primary photochemistry, equal to the efficiency by which an absorbed photon trapped by the PSII RC will result in reduction of Q_A to Q_A^-
$\psi Eo = ET_o/TR_o = (1 - V_j)$	The efficiency by which a trapped exciton, having triggered the reduction of Q_A to Q_A^- can move an electron further than Q_A^- into the intersystem electron transport chain
$\delta Ro = RE_o/ET_o = (1 - V_i)/(1 - V_j)$	The efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end acceptors
Performance index	
$PI_{abs} = [RC/ABS] \times [\phi Po/(1 - \phi Po)] \times [\psi Eo/(1 - \psi Eo)]$	Performance index on absorption basis, incorporating the steps from antenna, reaction center and electron transport parameters
$PI_{total} = [RC/ABS] \times [\phi Po/(1 - \phi Po)] \times [\psi Eo/(1 - \psi Eo)] \times [\delta Ro/(1 - \delta Ro)]$	Total performance index per absorption basis, integrates into the sum of changes in quantum yields and absorption

Table 2 The fluorescence parameters on four *Populus* species under CO₂ stress

Species	<i>Populus X</i>		<i>Populus deltoides</i> × <i>cathayana</i>		<i>Populus alba</i> 'Berdinensis' L.		<i>Populus euramericana</i> "N3016" × <i>Populus ussuriensis</i>	
Measured parameters	Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
<i>Fo</i>	2,798 ±171.57	2,345 ±166.19	2,576.75 ±116.56	2,643.6 ±96.32	2,284.4 ±75.49	2,065 ±98.63	2,282.75 ±66.48	2,298.25 ±280.5
<i>Fj</i>	7,314.33 ±640.30	6,703.5 ±323.45	7,325 ±508.27	7,493 ±686.81	6,314.8 ±362.77	6,051.33 ±323.15	6,492.50 ±104.95	6,325.25 ±111.60
<i>Fi</i>	12,332.67 ±258.46	11,909.5 ±310.17	12,008.5 ±194.37	12,669.4 ±75.86	11,297.4 ±233.28	10,267 ±282.20	11,315.25 ±252.66	10,889.25 ±219.88
<i>Fm</i>	16,725.67 ±1,263.26	13,462 ±782.00	16,936 ±580.53	15,267.8 ±878.34	14,546.2 ±1058.17	12,577.33 ±578.35	14,989.5 ±463.67	13,330.5 ±578.09
Derived parameters								
<i>Vj</i>	0.324 ±0.009	0.395 ±0.090	0.328 ±0.028	0.385 ±0.005	0.327 ±0.022	0.379 ±0.016	0.332 ±0.012	0.366 ±0.015
<i>Vi</i>	0.684 ±0.014	0.865 ±0.069	0.652 ±0.002	0.796 ±0.004	0.739 ±0.014	0.781 ±0.020	0.712 ±0.026	0.780 ±0.018
ABS/RC	0.756 ±0.009	0.896 ±0.037	0.782 ±0.008	0.767 ±0.013	0.860 ±0.017	1.009 ±0.024	0.829 ±0.008	0.851 ±0.008
$\phi Po = TRo/ABS = FV/FM$	0.833 ±0.002	0.825 ±0.001	0.848 ±0.002	0.826 ±0.009	0.842 ±0.004	0.836 ±0.005	0.848 ±0.003	0.827 ±0.01
$\Psi Eo = ETo/TRo$	0.676 ±0.009	0.605 ±0.042	0.672 ±0.027	0.615 ±0.024	0.673 ±0.021	0.621 ±0.016	0.668 ±0.012	0.634 ±0.015
ϕEo	0.563 ±0.006	0.500 ±0.008	0.570 ±0.013	0.508 ±0.019	0.567 ±0.018	0.519 ±0.016	0.566 ±0.017	0.525 ±0.018
<i>PIABS</i>	8.141 ±0.137	7.053 ±0.163	11.639 ±0.64	6.126 ±0.937	8.597 ±0.129	8.488 ±0.094	9.033 ±0.519	7.315 ±0.183
<i>PItotal</i>	2.134 ±0.0009	0.575 ±0.028	2.724 ±0.013	0.835 ±0.004	2.016 ±0.012	1.326 ±0.017	2.207 ±0.007	1.143 ±0.008

Note: Values of the mean ± standard error for the un-manipulated control are given. The parameters are, minimum fluorescence at 20 s, *Fo*; fluorescence intensity at 2 ms, *Fj*; fluorescence intensity at 30 ms, *Fi*; maximum fluorescence, *Fm*; relative variable fluorescence at the J-step, *Vj*; relative variable fluorescence at the I-step, *Vi*; measure of the average total absorbance per active PSII RC, ABS/RC; maximum quantum yield of primary photochemistry, $\phi Po (= TRo/ABS)$; probability that a trapped exciton moves an electron into the electron transport chain beyond QA-, *ETo/TRo*; total performance index per absorption basis, *PItotal* (see also Table 1). Results are presented as mean of five individual measurements

In summary, inhibition of PSII under high CO₂ stress has involved in changes of *Fm* and *PI_{total}*. In other words, these two parameters can be used to evaluate the state of PSII. These results also indicated that changes of PSII attribute to the degradation of antenna pigment and inhibition of the electron transport at the acceptor side of PSII.

3 Materials and Methods

3.1 Plant material and stress treatment

The experiments were carried out in College of Life Science, Northeast Forestry University from Harbin, Heilongjiang Province. Four *Populus* species (*populus X*, *Populus deltoides* × *cathayana*, *Populus alba* 'Berdinensis' and *Populus euramericana* 'N3016' × *Populus ussuriensis*) were used as experimental materials. The cuttings were grown in plastic pots (60 cm in length, 25 cm in breadth and 15cm in depth) filled with 1.5kg of soil and sand (2:1). There are 10 cuttings in each pot. Potted plants were grown in the conditions: day/night air temperature, 28/22 °C; photoperiod, 12h; relative humidity, 65-85%. One Chamber was kept at a CO₂ concentration (average±SD) of 370 ± 15 μmol/mol (control), while another chamber was treated with an elevated CO₂ concentration of 1500 ± 50 μmol/mol (treatment). At the 7th day after treatment, we examined the effect of EC on every variety of poplar using JIP-test. Ten biological replicates were repeated

3.2 Chlorophyll a fluorescence transient measurement and the JIP-test

The OJIP transients were measured using fully expanded leaves. All measurements were carried out between 13:00 and 15:00 in May, 2016. After the plants had been exposed to high and normal CO₂ concentration for 7 d, respectively, all leaves were exposed to a 30-min dark condition, before determination of OJIP transients. Accordingly, OJIP transients were measured using a portable chlorophyll a fluorometer (Hansatech Instruments, Ltd., King's Lynn Norfolk, UK). In addition, we calculated values of several JIP parameters according to the JIP-test equations based on the methods of Strasser et al., Strasser et al., Tsimilli-Michael and Strasser (Strasser et al., 2004; Strasser et al., 2010; Tsimilli-Michael and Strasser, 2008).

In general, there are four important inflection points on the fluorescence fast dynamic curve, namely the O - J - I - P turning point. They are: 1) O point shows that the system (PSI) release amount of the fluorescent light, which can be used as the light of the PSI and efficiency, the fluorescence intensity is at 0.02 ms (*F₀*). 2) Fluorescence intensity at 2ms is called *F_j*, J inflection point, which can reflect the reaction in the accumulation of the electron acceptor Q_A⁻ to Q_B⁻, the oxidation of the Q. 3) Fluorescence intensity at 30ms is called *F_i*. 4) Maximum fluorescence intensity is *F_m*.

3.3 Data analysis

Each experiment was conducted at least ten times independently. All data presented were mean values of each treatment.

Authors' contributions

Ruyu Xie, Mu Peng and Fanjuan Meng performed and designed the experiments; Tao Wang, Fanjuan Meng and Fachun Guan performed and analyzed the data.

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