

Effect of High CO₂ Concentration on Four *Populus* by the Fast Fluorescence Rise OJIP

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Abstract

Increased atmospheric carbon dioxide (CO₂) concentration affects plant physiological and ecosystem processes. The aim of this study was finding out the main reasons why PSII were affected by CO₂ in four different kinds of *Populus* (*Populus* L., *Populus* X, *Populus deltoides* × *cathayana*, *Populus alba* 'Berdinensis' L., *Populus euramerican* 'N3016' × *Populus ussuriensis*) and the differences of responses in these four kinds of *Populus*. The chlorophyll fluorescence technique was considered as an effective tool in the context of non-destructive leaf photosynthetic apparatus of the degree of thermal, and has been widely used in relevant studies of CO₂ stress. The JIP-test is a method for analyze the fluorescence transient which transformed the measured value to a serials biological parameters, and also detect the energy strength generated by PSII. The results show that the PSII performance was negatively influenced by CO₂ stress. CO₂ stress resulted in down-regulation of F_m , φ_{P_0} ($=F_v/F_m$), ψ_{E_0} , φ_{E_0} and PI_{total} in all 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 with high CO₂. So a fast decrease of the P-step level indicated there was main change to fluorescence transients. Generally speaking, these results indicated that the main reasons why PSII were affected by CO₂ were degradation of antenna pigment and inhibition of the electron transport at the acceptor side of PSII.

Keywords: Atmospheric Carbon Dioxide (CO₂); Photosynthetic Performance; *Populus* L.; OJIP

Introduction

Environmental changes caused by increased emissions of greenhouse gasses have influenced the stability of ecosystems worldwide [1]. The increase of atmospheric carbon dioxide (CO₂) is one of the most important environmental changes in the world in the past and the future. Especially, human activities also increased the concentration of CO₂ in the atmosphere, which is expected to reach 700 μL/L by the middle of the next century [2-5]. Current evidence showed the increase of CO₂ concentration will influence on plant growth, development biological yield. In general, high CO₂ concentrations increase photosynthetic rates, which promoted the growth of plants.

However, there are most reports on the response of crop plant species to elevated atmospheric CO₂, but few of them have given account of the response of woody species to high CO₂ levels. In this study, we compared the effect of elevated CO₂ on the growth

and photosynthetic characteristics of four *Populus* (*Populus* L.) species.

Populus spp., as poplar hybrids, belongs to a fastest-growing tree. For their rapid growth, their wood can be used for construction, pulp, paper, and as a renewable, cost-effective alternative to fossil fuels. Previous reports showed that poplars are sensitive to environmental stress compared with other tree species [6,7]. To date, the effects of high CO₂ levels on *Populus* physiology and growth have been studied in numerous researches. For example, in birch, elevated CO₂ treatments had no major impacts on wood anatomy or wood density [8]. Lee et al., (2014) found that the cuttings of *Populus alba* × *glandulosa* under the elevated CO₂ treatment showed reduced tree height and photosynthetic pigment contents such as chlorophyll and carotenoid. In particular, the elevated treatment resulted in a marked reduction in the chlorophyll a. However, some works also showed that increased CO₂ delayed leaf fall, but this effect is species-specific. However, there are few tests of whether differences in photosynthetic ability exist between different *Populus* species in response to elevated CO₂. Generally,

the photosynthetic ability was reported to a reliable indirect indicator of tree performances under different environmental stress [9,10].

As a rapid and non-destructive technique, this technology is very useful to investigate the photosynthetic function, and has been used to study the effects of drought, high temperature, salt stress on plant species. Additionally, this technology has also provided valuable information on the functional and structural attributes of components involved in photosynthetic electron transport and especially to study photosystem II (PSII) behavior [11- 21]. In general, a sequence of phases (labelled as O, K, J, I, P) can be obtained in the fluorescence rise during the first second of illumination from the initial (F_0) to the maximal (F_m) fluorescence value. This mathematical model was named as JIP-test, which can provide quantum yields, biophysical parameters and probabilities characterizing structure and function of PSII [22,23]. PSII is very sensitive to environmental stresses [9,10]. However, a complex study comparing influences of high CO₂ levels 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 using the fast Chl fluorescence records.

In our study, we have examined photosynthetic responses of four *Populus* spp. species to high CO₂ levels using fast Chlorophyll (Chl) a fluorescence transient (O-J-I-P) technology. In this study, we analyzed the transient fluorescence using JIP-test in 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 elevated atmospheric CO₂.

Materials and Methods

Plant Material and Stress Treatment

Experiments were performed at College of Life Science, Northeast Forestry University, which is located in Harbin, Heilongjiang Province. Four *Populus* species including *Populus* X, *Populus deltoides* × *cathayana*, *Populus alba* 'Berdinensis' L and *Populus euramericana* 'N3016' × *Populus ussuriensis* were used in the experiments.

The cuttings were planted in plastic pots (60 cm in length, 25 cm in breadth and 15 cm in depth) filled with 1.5 kg of soil and

sand (2: 1). The experiments were carried out in the close gas-exchange system consisting of chambers of 300 L volume (71cm in length, 73cm in breadth and 175 cm in height). 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 (hereafter denoted as treatment). In order to study the effect of CO₂ for every variety of poplar, we choose the seventh day after treatment to JIP-test in this study. We repeated the experiment three times with 10 plants in total, 10 for controls and 10 for elevated treatment.

Chlorophyll a Fluorescence Transient Measurement and the JIP-Test

JIP - test is a method to analyze the transient fluorescence, also known as fluorescence fast dynamic research method. Measuring the curve of rising flourespar light (FLR) (rapid fluorescence kinetics) needed very strict about equipment, and the light source for high strength of saturated excitation light (strong degrees in 3000 ~ 10000 μmol photons/ (m² s)), starting fast, and can quickly capture the fluorescence signal.

JIP - test is an important method of analysis of fluorescence kinetics curve, the purpose of this method is to turn the parameters of the measured values into a biological significance that can direct energy intensity produced by PSII. In general, there are four important inflection point on the fluorescence fast dynamic curve, namely the O - J - I - P turning point, respectively is: 1) O point shows that the system (PSI) release amount of the fluorescent light, which can be understood as the light of the PSI and efficiency, the fluorescence intensity is at 0.02 ms (F_0). 2) Fluorescence intensity at 2ms, called F_j , J inflection point 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 called F_i . 4) Maximum fluorescence intensity is F_m .

Leaves were dark adapted for 30 min to ensure that all PSII RCs were in the dark adapted state with open RCs. Then chlorophyll-a fluorescence transients were recorded and digitized with the portable Handy PEA (Hansatech Instruments, Ltd., King's Lynn Norfolk, UK) with a 12-bit resolution from 10 s to 1 s and a time resolution of 10 s for the first 200 data points (Strasser et al., 1995). All measured and derived parameters (Table 1) are based on Strasser et al. [24,25] and Tsimilli-Michael [26].

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 μ s
F_l	Fluorescence intensity at the L-step (100 μ s)
F_k	Fluorescence at the K-step (300 μ s)
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
$M_o = 4 \times (F_{300s} - F_o) / (F_m - F_o)$	Approximated initial slope per ms of the fluorescence transient
$ABS/RC = [M_o/V_j] \times [1/(F_v/F_m)]$	Measure of the average total absorbance per active PSII RC
Quantum yields	
$\varphi_{Po} = TR_o/ABS = (F_m - F_o)/F_m = F_v/F_m$	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	
$PI_{abs} = [RC/ABS] \times [\varphi_{Po}/(1 - \varphi_{Po})] \times [\psi_{Eo}/(1 - \psi_{Eo})]$	Performance index on absorption basis, incorporating the steps from antenna, reaction center and electron transport parameters
$PI_{total} = [RC/ABS] \times [\varphi_{Po}/(1 - \varphi_{Po})] \times [\psi_{Eo}/(1 - \psi_{Eo})] \times [\delta_{Ro}/(1 - \delta_{Ro})]$	Total performance index per absorption basis, integrates into the sum of changes in quantum yields and absorption

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

Poplar leaves can completely cover the fluorescent clip test hole, it can measure directly. The excitation light was red light whose intensity was 3000 $\mu\text{mol}/\text{m}^2\text{s}$ saturated light intensity with peak wavelength of 650 nm. Fluorescent signal recording time of 10s, each group of plant test repeat 5 times.

Date Analysis

Each experiment was conducted at least five times independently. All data presented were mean values of each treatment. Standard Errors (SE) for the values obtained were calculated. All the above data analyses were processed using SPSS17.0 Software.

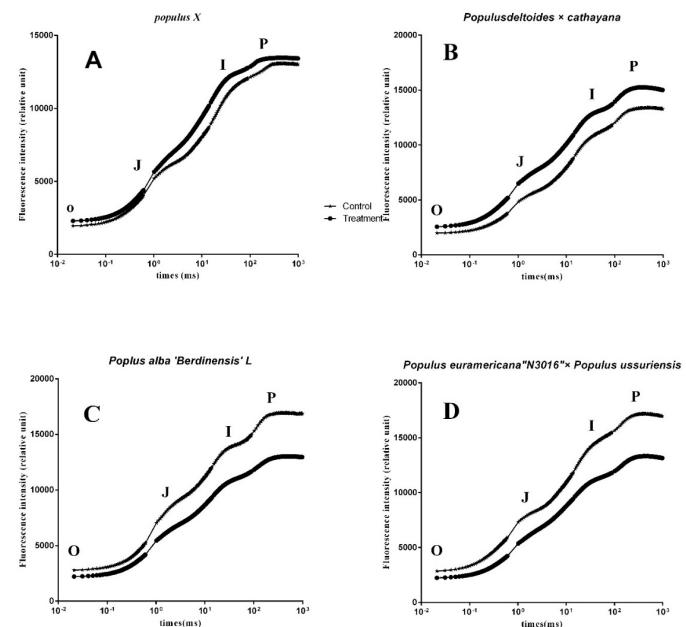
Results

Changes in Photosystem II (PS II) Under CO₂ Stress

In Figure 1, four typical O-J-I-P chlorophyll fluorescence transient in leaves of untreated and treated seedlings of four *Populus* species are shown. To analyze changes in the shape of the transients among all *Populus* genotypes, All O-J-I-P transients were normalized at the O- and P-step. In four genotypes the response of treated seedlings was not similar.

In *Populus X*, at the 7th day, relative fluorescence intensity was decreased (Figure 1A). Thus high CO₂ conditions after long time inhibited the fluorescence intensity, especially from I- to P- step of *Populus X*. In *Populus deltoides* × *cathayana*, at 7th day, relative fluorescence intensity was increased. While, relative fluorescence intensity was increased from J- to I- step (Figure 1B), which showed different changes from these genotypes in relative fluorescence intensity. In *Populus alba 'Berdinensis' L*, relative fluorescence intensity was similar between control and treatment from J- to I- step (Figure 1C). In *Populus euramericana 'N3016' × Populus ussuriensis*, an increase in relative fluorescence intensity was observed from I- to P- step (Figure 1D).

the efficiency with which the energy of a trapped exciton is converted into electron transport beyond Q_A (ϕ_{Eo}), the quantum yield of electron transport beyond Q_A (ϕ_{Eo}) and total performance index per absorption basis (PI_{total}) after high CO₂ treatment. Especially, PI_{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) of treated-plants were higher than those of controls. There is higher value in ABS/RC (measure of the average total absorbance per active PSII RC) of treated plants compared to those of control plants. However, an exception for the *Populus deltoides* × *cathayana* after treatment had no difference between CO₂-treated and control plants (Table 2).



Figures 1(A-D): 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.

Changes of Fluorescence Parameters Under CO₂ Stress

In Table 2, no significant high CO₂-induced 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). In parallel, all *Populus* species showed significant decrease in maximum quantum yield of PSII primary photochemistry (ϕ_{P0}),

Species	<i>Populus X</i>		<i>Populus deltoides</i> × <i>cathayana</i>		<i>Populus alba 'Berdinensis' L</i>		<i>Populus euramericana 'N3016' × Populus ussuriensis</i>	
Measured parameters	Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
F_o	2798±171 .57	2345± 166.19	2576.75± 116.56	2643.6± 96.32	2284.4± 75.49	2065±98.63	2282.75±66.48	2298.25±280.5

F_j	7314.33±640.30	6703.5±323.45	7325±508.27	7493±686.81	6314.8±362.77	6051.33±323.15	6492.50±104.95	6325.25±111.60
F_i	12332.67±258.46	11909.5±310.17	12008.5±194.37	12669.4±75.86	11297.4±233.28	10267±282.20	11315.25±252.66	10889.25±219.88
F_m	16725.67±1263.26	13462±782.00	16936±580.53	15267.8±878.34	14546.2±1058.17	12577.33±578.35	14989.5±463.67	13330.5±578.09
Derived parameters								
V_j	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
V_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
$\varphi_{Po} = TRo/ABS = F_v/F_m$	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
φ_{Eo}	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
PI_{ABS}	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
PI_{total}	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

Values of the mean ± standard error for the un-manipulated control are given. The parameters are, minimum fluorescence at 20 s, F_o ; fluorescence intensity at 2 ms, F_j ; fluorescence intensity at 30 ms, F_i ; maximum fluorescence, F_m ; relative variable fluorescence at the J-step, V_j ; relative variable fluorescence at the I-step, V_i ; measure of the average total absorbance per active PSII RC, ABS/RC; maximum quantum yield of primary photochemistry, φ_{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, PI_{total} (see also Table 1). Results are presented as mean of five individual measurements.

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

Discussion

In this study, the shapes of chlorophyll a fluorescence transient (O-J-I-P) were markedly different in the four high CO₂-treated leaves, 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 as similar F_v/F_m . Generally, the level of photochemical reaction can be evaluated according to the chlorophyll fluorescence intensity. And F_v/F_m was used to describe

the trapping efficiency of the absorbed light, which can reduce primary quinone electron acceptor of PSII (Q_A) [27]. Therefore, the different fluorescence transients of leaves under high CO₂ levels indicated that the photochemical reactions were different in 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 [28]. Various environmental stress can lead to inhibition of photosynthetic efficiency, accordingly, affecting state

of the photosynthetic apparatus.

For O-J-I-P, point O represents the fluorescence of PS II action center when 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 [29]. Here, higher J value in the leaves. In addition, point I reflects the heterogeneity of PQ, the electron acceptor state in point I mainly is related to Q_A⁻ and Q_B²⁻. 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 CO₂ 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 with high CO₂. So a fast decrease of the P-step level indicated 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_B²⁻ and PQH [30, 31].

No significant changes in F_o, F_j and F_i of different *Populus* species were observed when subjected to high CO₂ stress. However, high CO₂ stress result F_m in decrease. F_m reflects maximum fluorescence intensity at the P-step [32]. Therefore, this result suggested that the F_m may be a good marker of PSII vitality under CO₂ 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 [33]. One of parameters used to analyze the response of the plant's PSII is PI_{total}. PI_{total} is sensitive to changes in either antenna properties, trapping efficiency or electron transport beyond Q_A [34]. In this study, we found that PSII performance was represented using this index (PI_{total}). In general, the observed PI_{total} is influenced by changes in antenna, RC, electron transport and end-acceptor reduction dependent parameters. Thus, PI_{total} integrates the response of RC/ABS, TRo/ABS(=F_v/F_m), ET_o/TRo(= [1 - V_j]) and RE_o/ET_o(=[1 - V_i]/[1 - V_j]).

In summary, inhibition of PSII under CO₂ stress involved in changes of F_m and PI_{total}. In other words, these two parameters can be used to indicate the changes of PSII. These results indicated that the main reasons why PSII were affected by CO₂ were degradation of antenna pigment and inhibition of the electron transport at the acceptor side of PSII.

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Conflict of Interest

The authors declare that there are no conflicts of interest.

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