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RESEARCH PAPERS

Responses of Photosystem II of White Elm to UV-B Radiation Monitored by OJIP Fluorescence Transients[1]

X. L. Pan[a], D. Y. Zhang[b], and L. Li[a]

[a] *Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, 830011 China*

[b] *State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang, 550002 China;*

fax: +86-851-589-0459; e-mail: zhangdaoyong@vip.gyig.ac.cn

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Abstract—Photosystem II (PSII) activities in both samara and leaf of white elm (*Ulmus pumila* L.) were significantly inhibited by enhanced UV-B radiation (UVBR). UVBR disturbed both the donor and acceptor sides of PSII. The plastoquinone (PQ) pool size on the acceptor side, the trapped excited energy for complete reduction of Q_A, and the proportion of closed PSII reaction centers (RCs) increased, with PSII RCs being transformed into dissipative sinks for excitation energy under UVBR. However, samara and leaf responded to UVBR in different ways. A decrease in the F_0 for leaf induced by UV-B radiation suggests the formation of fluorescence-quenching centers. An increase in the V_I for leaf under UVBR might mean the accumulation of reduced Q_A and PQ. F_0 and V_I for samara showed opposite change pattern. Leaf has the mechanism of regulation of the amount of light reaching the RC through decreasing the number of light-harvesting chlorophyll molecules under UVBR while samara may be unable to regulate the light-harvesting capacity. PSII in samara was more susceptible to UVBR than that in leaf, with PI_{ABS} for samara decreasing more rapidly by a factor of 6.4 than that for leaf. Samara can recover more easily from UVBR-induced damage to PSII than the leaf.

Keywords: Ulmus pumila, samara, photosystem II, UV-B radiation, chlorophyll fluorescence.

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INTRODUCTION

White elm (*Ulmus pumila* L.) is widely found in the semi-arid and arid regions of China. It is an important hardwood with high economic value. Its fruit is a disc-like samara, being composed of a compressed nutlet (seed) surrounded by a membranous wing. The seed is centrally embedded in the wings. The function of a samara's wing is to enable the seed to be dispersed over a large distance by wind, providing the tree with an evolutionary advantage. Since the seed is embedded in the wings, the photosynthetic performance in samara wings should be closely related with the quality of the seed inside. However, information on the photosynthesis of the samara was lack possibly because samara is not easily available due to the short flowering period.

In the semi-arid and arid regions of China, the solar ultraviolet (UV) irradiation reaching the earth's surface is kept at high levels for most time. Among the UV irradiation, UV-B (280–315 nm) radiation level is also high. What is more important, the solar UV-B radiation at the earth's surface shows an increasing trend due to an accelerating depletion of stratospheric ozone. The increasing UV-B radiation now is an important environmental stressor for plants in semi-arid and arid lands.

The enhanced UV-B radiation (UVBR) has adverse impact on algae and higher plants [1–6]. The photosynthetic apparatus is one of the primary target sites for UVBR. UVBR reduces photochemical activity in photosystem II (PSII) by damaging the photosynthetic apparatus at multiple sites, including the D1 and D2 proteins [1–3, 5].

However, in the case of white elm, limited information is available on the effects of enhanced UVBR on its photosynthetic physiology, especially the electron transport and energy flux in PSII in samara, despite its important role in population development in semi-arid and arid regions.

When illuminated with high intensity actinic light, dark-adapted oxygenic photosynthetic organisms show the polyphasic rise with the basic steps from the origin (O) through two inflections (J and I) to a peak fluorescence level (P) [7]. The fast Chl *a* fluorescence (O-J-I-P) rise transient was generally believed to provide important information on the photochemical activity of PSII and the associated filling of the plasto-

[1] This text was submitted by the authors in English.

Abbreviations: Chl—chlorophyll; PSII—photosystem II; PQ—plastoquinone; RC—reaction center; UVBR—UV-B radiation.

quinone (PQ) pool [7] established a procedure for quantitatively calculating several phenomenological and biophysical parameters on the basis of the O-J-I-P fluorescence transient, known as the JIP-test. The JIP-test has been proved to be a useful tool for in vivo investigation of PSII function under various environmental stresses [7].

In this study, effect of enhanced UVBR on PSII activity in white elm samara and leaf were comparatively studied by measuring in vivo fast Chl *a* fluorescence rise transient and JIP-test. The objectives of this study were to (1) compare the responses of PSII activity between samara and leaf to enhanced UVBR, (2) elucidate the mechanism involved in the effect of enhanced UVBR on PSII in samara and leaf, and (3) assess recovery potential of the damage to PSII function induced by UVBR.

MATERIALS AND METHODS

Plant material. White elm (*Ulmus pumila* L.) shoot cuttings (30-cm-long) with dozens of two-week-old samaras and leaves were collected from Xinjiang Branch of Chinese Academy of Sciences, Urumqi, China. Immediately after the cuttings were obtained, they were placed into glass containers containing 10-cm-deep tap water with the leaves and samaras being not immersed in water. The glass containers then were placed in a growth chamber with photosynthetic photon flux density (PPFD) of 300 μmol/(m^2 s) and temperature of 22–25°C. The chlorophyll fluorescence of samaras and leaves was monitored every hour. The values of the JIP-test parameters for samaras and leaves of cuttings kept in the tap water changed little for at least two days. Therefore, tap water was used as the supporting medium for cuttings in all experiments. The cuttings without application of enhanced UVBR were used as the control. The samaras and leaves were continuously exposed to enhanced UVBR. Three pieces of samaras or leaves were randomly picked periodically for chlorophyll fluorescence tests.

UVBR treatment. Ultraviolet-B radiation was provided by UVB bulbs with λ_{max} = 313 nm (Jinhua Instrument, Jiangshu, China) and spectral interval of 280–315 nm, which was filtered through cellulose acetate sheeting. The UVBR was at 0.6 W/m^2. The UV intensity was measured with a UV radiometer (TN-2340, Taiwan, China). The radiation time was up to 30 min. Chlorophyll fluorescence of samaras and leaves after exposure to UVBR for different time were determined.

Polyphasic fast fluorescence induction and JIP-test. Samples (samaras and leaves) were adapted in the dark for 5 min before measurement of chlorophyll fluorescence. The chlorophyll fluorescence transient was recorded up to 1 s on a logarithmic time scale, with a data acquisition every 10 μs for the first 2 ms and every 1 ms thereafter, using FL100b (Brno, Czech Republic). Each measured O-J-I-P induction curve was analyzed according to the JIP-test [7]. The following data were directly obtained from the fast rise kinetic curves: F_0, the initial fluorescence, was measured at 50 μs, when all reaction centers (RCs) are open; F_J and F_I are the fluorescence intensity at J step (at 2 ms) and I step (at 30 ms), respectively; F_M, the maximal fluorescence, was the peak fluorescence at P step when all RCs were closed after illumination; $F_{300\,\mu s}$ was the fluorescence at 300 μs. Selected JIP-test parameters quantifying PSII behavior were calculated from the above original data after the formulae presented in Table 1 [7].

Statistics. All experiments were repeated at least three times, and the results were presented as mean or mean ± SE (standard error). Student's *t*-test was used for statistical analysis of experimental data. Statistical significance was accepted when $p \le 0.05$.

RESULTS AND DISCUSSION

Effect of UVBR on Fluorescence Rise O-J-I-P Kinetics

The O-J-I-P fluorescence transient reflects the state of Q_A, Q_B, and PQ pool. Figure 1 shows the representative fast kinetic induction curves of the control and the samples under UVBR for 30 min. The JIP-test parameters for leaves and samaras under UV-B radiation for different time are summarized in Table 2. It was found that the whole O-J-I-P curves for samaras were above those for leaves, regardless of the sample treated or untreated with UVBR. UVBR persistently decreased F_M for both samaras and leaves, accompanied by an increase in the relative variable fluorescence intensity at the J-step (V_J). The decreasing of F_M might be interpreted as an increase in the proportion of the closed PSII RCs, which did not participate in electron transport. The increase in V_J might indicate a rise in the proportion of closed PSII RCs and consequently in the proportion of reduced Q_A at J step. Interestingly, the minimum fluorescence (F_0) and the relative variable fluorescence at I step (V_I) for samaras responded to UVBR contrary to those for leaves. F_0 for leaves was decreased by UVBR but increased for samaras. Several earlier studies also reported F_0 decreased during exposure to UVBR. F_0 quenching by UV radiation in leaves might be due to the formation of fluorescence-quenching centers within PSII under UV radiation. The increase of F_0 indicates the photoinhibition correlating with the occurrence of RCs with damage at the acceptor side of PSII. The increase in V_I for leaves due to UVBR indicates the accumulation of reduced Q_A and PQ, which cannot transfer electrons to the dark reactions. The contrary responses of F_0 and V_I to UVBR in leaves and samaras suggest that different mechanisms were involved in the effects of enhanced UVBR on PSII function for leaves and samaras.

Effect of UVBR on Photosynthetic Efficiency

For samaras, F_V, F_V/F_0, and F_V/F_M decreased drastically during the first 20 min of UVBR, resulting from

Table 1. Formulae and terms used in the JIP-test [7]

Formulae and terms	Illustrations
$V_j = (F_{2\,ms} - F_0)/(F_m - F_0)$	relative variable fluorescence intensity at the J step
$M_0 = 4(F_{300\,\mu s} - F_0)/(F_m - F_0)$	approximated initial slope of the fluorescence transient
$S_M = \text{area}/(F_M - F_0)$	working integral of the energy needed to close all RCs
$N = S_M M_0/V_J$	the turnover number indicates how much time Q_A has been reduced to Q_A^- in the time span from t_0 to t_{F_M}
$\varphi_{P0} = TR_0/ABS = [1 - (F_0/F_m)] = F_V/F_m$	maximum quantum yield for primary photochemistry (at t =0)
$\varphi_{E0} = ET_0/ABS = [1 - (F_0/F_m)]\Psi_0$	quantum yield for electron transport (at $t = 0$)
$\Psi_0 = ET_0/TR_0 = (1 - V_J)$	probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A (at $t = 0$)
$ABS/RC = M_0(1/V_J)(1/\varphi_{P0})$	absorption flux per RC
$TR_0/RC = M_0(1/V_J)$	trapped energy flux per RC (at $t = 0$)
$ET_0/RC = M_0(1/V_J)\Psi_0$	electron transport flux per RC (at $t = 0$)
$DI_0/RC = (ABS/RC) - (TR_0/RC)$	dissipated energy flux per RC (at $t = 0$)
$ABS/CS = ABS/CS_{Chl} = Chl/CS$	absorption flux per cross-section (at $t = 0$)
$PI_{ABS} = (RC/ABS)[\varphi_{P0}(1 - \varphi_{P0})]$ $[\Psi_0/(1 - \Psi_0)]$	performance index on absorption basis

Table 2. JIP-test parameters for samara and leaf under UVBR for different time period

Parameter	Samara				Leaf			
	1 min	10 min	20 min	30 min	1 min	10 min	20 min	30 min
F_M	2082	1734	1757	1681	1537	1360	1219	1151
F_0	446	469	607	579	281	274	252	253
F_V	1636	1265	1150	1102	1256	1086	967	898
F_V/F_m	0.786	0.730	0.655	0.656	0.817	0.799	0.793	0.780
F_V/F_0	3.668	2.697	1.895	1.903	4.470	3.964	3.837	3.549
V_J	0.519	0.563	0.580	0.586	0.431	0.460	0.469	0.486
V_I	0.779	0.764	0.757	0.744	0.662	0.679	0.675	0.706
PI_{ABS}	1.095	0.633	0.356	0.368	2.928	2.295	2.181	1.710
ψ_0	0.481	0.437	0.420	0.414	0.569	0.540	0.531	0.514
φE_0	0.378	0.319	0.275	0.271	0.465	0.431	0.421	0.401
S_M	558.0	584.8	861.3	709.7	559.3	546.1	683.8	673.7
N	1361.8	1412.8	2174.6	1696.3	922.3	882.5	1078.5	1155.9
ABS/RC	3.106	2.018	3.106	2.018	3.311	2.024	3.311	2.024
TR_0/RC	2.441	2.416	2.525	2.390	1.649	1.616	1.577	1.716
DI_0/RC	0.665	0.896	1.333	1.256	0.369	0.408	0.411	0.483
ET_0/RC	1.174	1.056	1.060	0.989	0.939	0.872	0.837	0.883

a decrease in F_M and an increase in F_0, and then changed little during the following 10 min of UVBR. For leaves, although F_0 increased slightly, the drastic decrease in F_M still caused slow and persistent decreases in F_V, F_V/F_0, and F_V/F_M with UVBR time. The lowering of F_V implies the lowered PSII capacity to reduce PQ, which might be attributed to the disturbance in the PSII donor side or the damage to the oxygen-evolving system. The decrease in F_V/F_0 suggests that photosynthetic process on the donor side of the PSII might be disrupted and water-splitting site might be severely impaired by UVBR. Performance index (PI_{ABS}) showed the same change patterns as F_V/F_M under UVBR. Responses of F_V/F_M and PI_{ABS} indicate

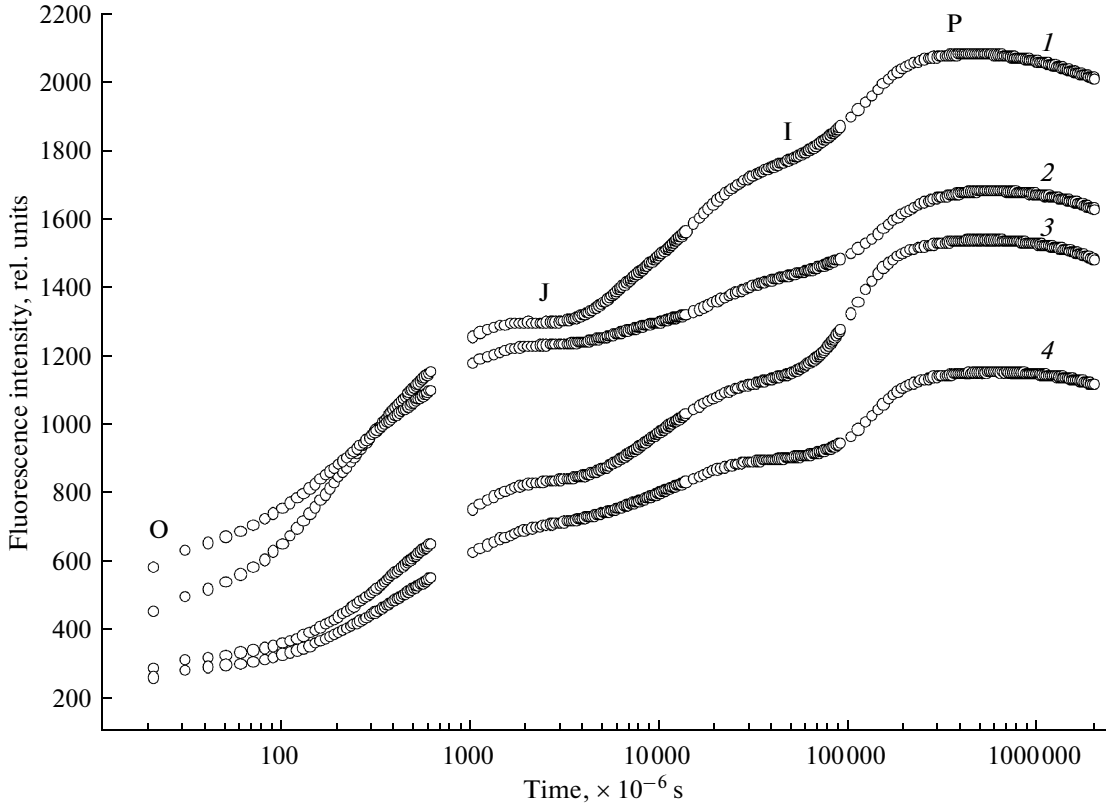

Fig. 1. Representative OJIP curves for samara and leaf treated and untreated with UVBR.
(*1*) Samara before UV-B radiation; (*2*) samara after 30-min UV-B radiation; (*3*) leaf before UV-B radiation; (*4*) leaf after 30-min UV-B radiation.

that samara was more sensitive to enhanced UVBR. The decreasing of maximum quantum yield for primary photochemistry (F_V/F_M) due to enhanced UVBR is in agreement with a few previous studies [8]. However, Sullivan et al. [9] showed that F_V/F_M was increased under UVBR in sweet gum. F_V/F_M was also found to remain unaffected for sea buckthorn (*Hippophae rhamnoides* L.) under UV radiation, while F_0, F_M, Y, and q_P were significantly decreased [10].

Effect of UVBR on Electron Transport

Effect of UVBR on the electron transport on the acceptor side of PSII was evaluated. The probability of electron transfer beyond $Q_A(\psi_0)$ and the yield of electron transport beyond Q_A (φE_0) for both samaras and leaves decreased with UVBR time, suggesting that UVBR rapidly inhibited electron transport on the acceptor side. S_M showed an increase trend over the UVBR time, indicating that the PQ pool on the acceptor side might increase and more energy was required for complete reduction of Q_A under UVBR. The turnover number, N, showed the same trend as S_M. A few previous studies also reported that the primary target for PSII damage by UVB is the acceptor side. Rodrigues et al. [11] showed that UVBR inhibited electron transport in PSII by damaging the quinone electron acceptors' redox function. On the contrary, some studies showed that the donor side, particularly at the water-oxidizing complex, was the primary target site for UV-B [12]. Other studies revealed that both the donor side and the acceptor side (near the Q_B site) were sensitive to UV-B [13, 14]. Van Rensen et al. [14] showed that UV-B firstly damaged the acceptor side of PSII for leaves of *Chenopodium album* and the donor side later. Vass et al. [13] reported that both the donor and acceptor sides of PSII were affected by UVBR, with the donor side being more sensitive.

Effect of UVBR on Energy Flux

For samara, the functional antenna size (ABS/RC) increased rapidly during the first 20 min of UVBR and decreased slightly during the following 10 min. In the case of the leaf, the value of ABS/RC changed little during the first 20 min of UVBR and increased significantly with prolonged UVBR. This result may indicate that samara is not able to regulate the light-harvesting capacity in order to adapt to UVB radiation, whereas the leaf has the mechanism of regulation of the amount of light reaching the RC through decreasing the number of light-harvesting Chl molecules

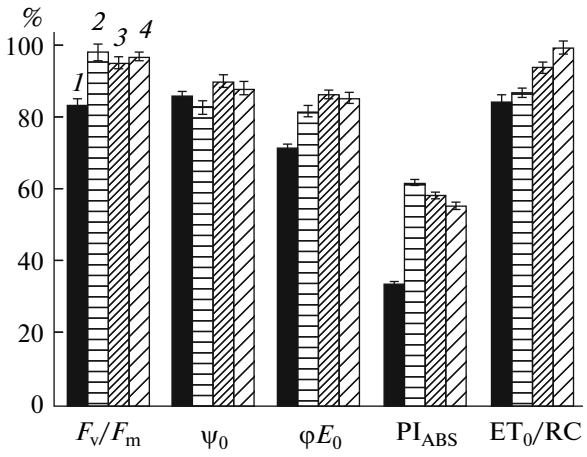

Fig. 2. Change of PSII functional parameters for samara and leaf after 30-min UVBR and 2-h recovery after cessation of UVBR.

(*1*) Samara after 30-min UV-B radiation; (*2*) samara after 2-h recovery; (*3*) leaf after 30-min UV-B radiation; (*4*) leaf after 2-h recovery.

All the values are expressed as the percentage of the control.

under moderate UVBR. This point may be further explained by the similar change of F_0 for samara and leaf. The increasing of F_0 for samara during the first 20 min of UVBR may also suggest the decreased efficiency of energy transfer from the antenna chlorophyll *a* to the RCs and/or the inactivation of PSII RCs. On the contrary, the decreasing of F_0 for leaf under UVBR during the first 20 min may indicate that nonfunctional PSII centers act as dissipative sinks.

No significant change of the trapping rate of the RC (TR_0/RC) for both samara and leaf under UVBR was observed. The changes of ABS/RC and TR_0/RC resulted in the same change pattern of the dissipation energy ($DI_0/RC = ABS/RC - TR_0/RC$). An increase in ABS/RC by 17.4 and 0.9% for samara and leaf led to the increase in DI_0/RC by 88.9 and 30.9% for samara and leaf, respectively. The increase in DI_0/RC suggests that PSII RCs are transformed into dissipative sinks for excitation energy under UVBR. ET_0/RC, related to the reoxidation of reduced Q_A via electron transport in an active RC, declined over UVBR time for samara and leaf. Since ET_0/RC is calculated as $TR_0/RC\psi_0$ and no significant change in TR_0/RC is observed, the decline in ET_0/RC mostly results from a decrease in the electron transfer beyond $Q_A(\psi_0)$, not from a decrease in TR_0/RC. Chow et al. [15] showed that dissipation rate increased drastically under a few hours of UVB exposure. Since $PSII_\beta$ centers with small antenna size and poor mutual energetic connectivity usually increase under various stresses [16], the increase of DI_0/RC might be due to increases of the $PSII_\beta$ centers and absorption cross section of PSII.

The light-induced inactivation of PSII firstly occurs at the oxygen-evolving site of PSII and then at the photochemical reaction center of PSII. Ohnishi et al. [17] observed that UV inactivated the oxygen-evolving complex much faster than the photochemical RC of PSII. On the other hand, light can inevitably produce various ROS, including H_2O_2 and singlet oxygen. Normally, the antioxidant systems can reduce these various ROS to tolerable levels. However, when PSII RCs are transformed into dissipative sinks for excitation energy under excess light, the production of ROS is accelerated and elevated levels of ROS give rise to oxidative stress [18]. The oxidative stress may overreduce Q_A [19] and inhibit the de novo synthesis of proteins and D1 protein, which are required for the repair of PSII [2]. Thus, excess light damages PSII directly, and the ROS produced inhibit the repair of PSII [3, 5, 20].

In addition to the aforementioned mechanisms, UVBR may also inhibit the synthesis of chlorophyll and carotenoids and alter the structure of the chloroplasts [21].

Recovery of PSII Function from Damage Induced by UVBR

Figure 2 shows the 2-h recovery of selected JIP-test parameters for 30-min UVBR treated samaras and leaves. For samara, F_V/F_M, PI_{ABS}, ET_0/RC, and φE_0 were recovered by 14.7, 28.5, 2.7, and 9.8% after cessation of UVBR for 2 h, respectively. However, ψ_0 continued to decrease by 3% after cessation of UVBR, implying that the electron transport chain beyond Q_A might not be repaired. For leaf, PSII functional parameters were less reduced under UVBR but also recovered less than those for samara. Only F_V/F_M and ET_0/RC recovered by 1.5 and 5.5%, respectively, after 2-h recovery, whereas PI_{ABS}, ψ_0, and ψE_0 continued to drop to lower values after cessation of UVBR. The lowering of PI_{ABS} suggests that damage to absorption of light energy, trapping of excitation energy, and conversion of excitation energy to electron transport in the leaf could not be reversed. This implies that, despite the recovery of the maximum quantum yield for primary photochemistry for leaf, some functions, such as electron transport in PSII, may still remain damaged, and could not be repaired. In addition, this result suggested PSII in samara was damaged in a different way from the leaf. PSII in samara was more sensitive to UVBR but also more easily recovered than that in the leaf. PSII in the leaf instead is more tolerant to UVBR and once it was damaged it cannot be reversed. The high recovery potential of PSII activity in samaras from UVBR is of ecological importance since they are seeds of elm.

The capacity of recovery from UVBR-induced damage to PSII was species-dependent and relevant to the physiological status of the leaves. Pradhan et al. [22] reported that, during its developing phase of

growth, the leaf could fully recover from UV-B-induced damage to PSII while the capacity to recover from the damage in fully developed leaves was reduced. Sfichi-Duke et al. [23] showed that PSII activity was recovered from the UV-B-induced damage in the wild-type *Scenedesmus obliquus* but not in the chlorophyll *b*-less mutant. Strid et al. [1] reported that recovery of the integrity of thylakoid membranes was very slow, implying a partial uncoupling of ATP synthesis from electron transport. The steps of PSII repair include the degradation of D1 protein, the synthesis of pre-D1, the assembly of the PSII complex, and the processing of pre-D1 [24]. Therefore, recovery from UV-induced damage to PSII could decrease productivity by increased demands on cell resources and protein synthesis during the recovery phase [21].

Conclusively, the present study clearly demonstrated that UVBR significantly and rapidly inhibited PSII activities in both samara and leaf of *U. pumila*. UVBR disturbed both the donor and acceptor sides of PSII. The PQ pool size on the acceptor side, the trapped excited energy for complete reduction of Q_A, and the proportion of closed PSII RCs increased, with PSII RCs being transformed into dissipative sinks for excitation energy under UVBR. However, samara and leaf responded to UVBR in different ways. For leaf, F_0 decreased and V_I increased under UVBR, indicating the formation of fluorescence-quenching centers, accumulation of reduced Q_A and PQ. For samara, F_0 increased and V_I decreased under UVBR. Leaf has the mechanism of regulation of the amount of light reaching the RC through decreasing the number of light-harvesting Chl molecules under moderate exposure of UVBR, while samara is unable to regulate the light-harvesting capacity. PSII in samara is more sensitive to UVBR than that in leaf. PSII in samara recovers more easily than that in leaf. The easy recovery of PSII activity in samaras from UVBR is of ecological importance in population establishment.

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