DOI: 10.32615/ps.2019.050 PHOTOSYNTHETICA 57 (2): 688-697, 2019

Effects of Pb and Zn toxicity on chlorophyll fluorescence and biomass production of *Koelreuteria paniculata* and *Zelkova schneideriana* young plants

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Abstract

The influence of Pb and Zn on chlorophyll (Chl) fluorescence and plant growth of one-year-old *Koelreuteria paniculata* and *Zelkova schneideriana* young plants was investigated. Pb and Zn contents in plant organs were measured. The results showed Pb and Zn stress decreased photochemical quenching and quantum efficiency of PSII, but increased energy dissipation in the tested plants. At the same time, maximum net photosynthetic rate, maximum quantum use efficiency, and organ biomass were reduced. Under the same concentration of heavy metals, the damage induced by Zn toxicity was more serious than that of Pb. Pb was less accumulated in leaves, with a mild effect on photosynthesis. Zn was mostly accumulated in leaves and strongly disturbed chloroplast functioning and affected photosynthesis. Pb and Zn had different pathway to influence biomass production, and both tested plants might use different mechanisms of action for heavy metal stress resistance.

Additional key words: bioconcentration factor; Pb toxicity; translocation factor; woody plant; Zn toxicity.

Introduction

Heavy metals often occur in trace concentrations naturally, but they may be concentrated in certain areas as a result of anthropogenic activities including burning of fossil fuels, mining, application of fertilizers and pesticides, industrial wastes, and vehicle emissions. The excess heavy metals have been recognized to have a significant toxicity for animals, plants, microorganisms, and human beings, as well as for environment (Nagajyoti *et al.* 2010, Sun *et al.* 2010, Lee *et al.* 2014, Shen *et al.* 2017, He *et al.* 2018). In southern China, lead (Pb) and zinc (Zn) were the most common heavy metal pollutants in soil (Sun *et al.* 2010, Hladun *et al.* 2016) and the concentrations of these two metals were much higher in this region than the standard criteria of the country (MEPC 2011). For instance, the mean contents of Pb and Zn were 179.6 and 67.7 mg kg^{-1}, respectively, in Quanzhou Bay of Fujian Province, whereas 107.3 and 162.6 mg kg^{-1}, respectively, in Nanjing of Jiangsu Province, which greatly exceeded the mean values in China (26.0 and 74.2 mg kg^{-1} for Pb and Zn, respectively) (Cheng 2003, Lu *et al.* 2003, Yu *et al.* 2008). The high concentrations of Pb and Zn pollution in Hunan province, one of the five top provinces for nonferrous metals production in China, have resulted in a series of environmental problems at local and regional scales (Hu *et al.* 2014, Chai *et al.* 2017). Hence, heavy metal pollution has become a critical problem in southern China and raised public concern.

Photosynthesis, a process in which light energy is used to produce sugar and other organic compounds, is sensitive to heavy metal stress (Cheng *et al.* 2003, Qiao *et al.* 2012). It was reported that Pb and Zn might inhibit the formation of the grana and electron transfer, suppress enzyme activity of PSII and enzymes of the Calvin cycle, and ultimately inhibit the photosynthesis process (Islam *et al.* 2008, Hu *et al.* 2012). Under high Pb and Zn concentrations, the photochemical efficiency of PSII was damaged (Baccio

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Received 15 October 2018, *accepted* 21 February 2019.

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Abbreviations: BCF – bioconcentration factor; F_0 – minimal fluorescence yield of the dark-adapted state; F_0' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_s – steady-state fluorescence yield; F_v – variable fluorescence; F_v/F_m – maximum quantum use efficiency; P_N – maximum net photosynthetic rate; q_L – photochemical quenching; TF – translocation factor; Y_{II} – quantum efficiency of PSII; Y_{NO} – quantum yield of nonregulated energy dissipation; Y_{NPQ} – quantum yield of regulated energy dissipation.

Acknowledgments: The authors thank '948' Introduction Project of The State Bureaucracy of Forestry (2014-4-62) Hunan Provincial Innovation Foundation For Postgraduate (CX2018B434), Scientific Innovation Fund for Post-graduates of Central South University of Forestry and Technology (20181007) and Nature Science Foundation of Hunan Provincial Innovative Research Team (2013) for the financial support.

et al. 2003, Romanowska *et al.* 2006). Ali *et al.* (1999) found inhibition of photosynthetic activity induced by high Zn concentrations in *Bacopa monniera*. Van Assche and Clijsters (1986) observed that Zn was accumulated in leaves of *Phaseolus vulgaris* and affected metabolic processes in the chloroplasts, such as electron transport and CO_2 fixation. Romanowska *et al.* (2006) pointed out that Pb induced a greater reduction in photosynthetic rate in pea plants due to the damages on both the photosystems and chloroplast ATPase activities.

Chl *a* fluorescence kinetics has been widely used to detect and analyze electron transport, absorption and conversion of light energy, photochemical efficiency of reaction center, dissipation of excess energy in photosynthesis process, especially in PSII activity under environmental stress conditions (Lavergne and Trissl 1995, Maxwell and Johnson 2000, Živčák *et al.* 2014, Guo and Tan 2015). Numerous studies have been carried out to examine the responses of Chl fluorescence parameters to Pb and Zn stress in herbaceous plants and crops (Harris *et al.* 1986, Sgardelis *et al.* 1994, Fu and Wang 2015, Rodriguez *et al.* 2015) and woody plants (Liu *et al.* 2007, Bao *et al.* 2016). Under the Pb and Zn stress, the electron transports of PSII (ETR), photochemical quenching (q_P), and maximum quantum use efficiency (F_v/F_m) decreased and nonphotochemical quenching (NPQ) increased. Recently, several new parameters were introduced into the method of Chl fluorescence to describe the status of energy balance and allocation in photosystems (Kramer *et al.* 2004). A number of studies have employed this method to examine tolerance characteristics of plants under drought (Yang *et al.* 2016), light acclimation (Wyber *et al.* 2017), saline stress (Yuan *et al.* 2014), and heat tolerance (Wang *et al.* 2009). But less is known about energy balance, allocation of PSII and fraction of excitons trapped by NPQ pathway in woody plants under Pb and Zn stress.

Koelreuteria paniculata and *Zelkova schneideriana* are important valuable timber tree species in southern China with characteristics of excellent wood quality, and strong stress resistance and ecological adaptability (Dou *et al.* 1999, Huang *et al.* 2001). Despite *K. paniculata* and *Z. schneideriana* were shown to have a high tolerance to Mn- and Cd-contaminated environments (Fang *et al.* 2007, Yang *et al.* 2017), the influence of Pb and Zn stress on photosystem function and photosynthetic process of *K. paniculata* and *Z. schneideriana* has not been studied.

The purpose of this paper was to examine photosynthetic responses of *K. paniculata* and *Z. schneideriana* under Pb and Zn stress. The specific objectives of the research project were: (*1*) to determine the changes of energy balance and allocation in PSII function under Pb and Zn stress, (*2*) to assess the short-term influence of Pb and Zn on growth and biomass production of *K. paniculata* and *Z. schneideriana* young plants, (*3*) to describe the distribution of the two heavy metals in various plant organs, and (*4*) to develop the relationships between leaf biomass and photosynthetic performance and heavy metal accumulation. We hypothesized that Pb, a nonessential element for plant growth and development, would be less transported to plant leaves than Zn. We further hypothesized that as an essential micronutrient in plant life, Zn could be largely absorbed, transported, and accumulated in leaves than Pb, which might result in more serious damage of photosynthetic performance.

Materials and methods

Growth conditions and experimental setup: The experiment was conducted in a greenhouse at Central South University of Forestry and Technology (CSUFT), Hunan Province, China (28°8'12"N, 112°59'36"E,). The temperatures of the greenhouse were set at 28/20°C (day temperature for 10 h/night temperature for 14 h) and relative humidity was 65/85% during the study period. Noncontaminated soil (natural soil used in this experiment) was collected from the top layer (0–20 cm) in a field station of the CSUFT campus, then dried and passed through a 5-mm sieve. The physicochemical properties of the soil included 12.13 g(total C) kg^{-1}, 0.24 g(total N) kg^{-1}, 0.16 g(total P) kg^{-1}, pH 6.40, and Pb and Zn concentrations of 0.02 and 0.03 g kg^{-1}, respectively.

One-year-old young plants of *Koelreuteria paniculata* (mean height: ~ 84.1 cm, mean ground diameter: ~ 7.3 cm) and *Zelkova schneideriana* (mean height: ~ 91.2 cm, mean ground diameter: ~ 8.9 cm) were collected from a local nursery. One seedling was transplanted to a pot with ~ 9 kg of air-dried and noncontaminated soil. After transplantation, the pot was kept in the greenhouse for 90 d before Pb and Zn treatment started. A total of 70 pots were used in the experiment with 35 pots for each plant species.

Four concentrations of Pb and Zn were used in this experiment. They were at the concentration of 0, 500, 600, and 900 mg(Pb or Zn) kg^{-1} using $PbCl_2$ or $ZnCl_2$, respectively, designed correspondingly as control (CK), L1, L2, and L3 for Pb and Zn treatments, respectively. The level of contamination was determined on the basis of the previous studies (Riley and Zachara 1992, NJDEP 1996, CNEPA 2008, Yun *et al.* 2012, Lan *et al.* 2014). Ninety days after transplantation, according to the three concentrations of Pb and Zn, $PbCl_2$ and $ZnCl_2$ were used as aqueous solutions, respectively. About 400 mL of heavy metal solution was carefully added into the soil of each pot in treated groups in order to avoid contact with organs of tested plants. Distilled water of 400 mL was added to each pot in control groups. Each of Pb and Zn treatments had five replications. During the experiments, each pot was watered by 400 mL of distilled water every 3–4 d. All pots were weeded and the soil was loosen in them once a week.

Plant biomass: The treatment lasted for 15 d. At the end of the treatment (referred to as 15 d post-treatment), all plants were harvested for biomass measurement. The plant was divided into leaves, stem, and root components, oven-dried at 105°C for 15 min, and then dried at 70°C until constant mass was reached. The dry mass (DM) of each component was determined.

Total metal content: For the determination of the metal content, the dried biomass of the different organs was powdered and passed through 80-mesh sieves. Precisely

100 mg of plant material was placed into clean digestion tubes for digestion with 1 mL of HNO_3 and H_2O_2 (8:2, v/v) on a heating block at 180°C for 1 h, and subsequently at 200°C for 45–60 min in order to evaporate the samples to dryness. The residue was taken up in 10 mL of demineralized water. Both Pb and Zn concentrations were measured by atomic absorption spectrophotometry (*AA-6800*, *Shimadzu*, Kyoto, Japan) and provided on dry mass (DM). Each sample was analyzed three times, and the mean value was calculated (Wu *et al*. 2015).

The bioconcentration factor (BCF) reflects the ability of plants to accumulate metals and is defined ccording to Zhou *et al* (2013) and Andrejić *et al*. (2018) as: BCF = (concentration of Pb or Zn in plant tissues)/(concentration of Pb or Zn in soil). The translocation factor (TF) reflects the ability of plants to translocate metals and is defined as in Zhou *et al*. (2013): TF = (concentration of Pb or Zn in plant aerial parts)/(concentration of Pb or Zn in roots).

Maximum net photosynthetic rate and Chl fluorescence parameters: Maximum net photosynthetic rate (P_N) was measured using a *Li-6400* portable photosynthesis system (*LI-COR 6400*, Lincoln, USA). The measurement conditions were set up as: leaf temperature of 25–32°C and PAR of 1,000 µmol(photon) m^{-2} s^{-1}. After 15 d of treatment, the photosynthetic parameters were measured on a clear day. Three young, healthy, and fully expanded leaves of similar size were selected from each seedling for the measurements of photosynthesis.

Chl fluorescence parameters including photochemical quenching (q_L), quantum efficiency of PSII (Y_{II}), quantum yield of regulated energy dissipation (Y_{NPQ}), maximum quantum use efficiency (F_v/F_m), non-light-induced energy dissipation (Y_{NO}) were measured by imaging a pulse amplitude modulation Chl fluorometer *MINI-PAM* (*Walz*, Effeltrich, Germany). The measuring procedure was as follows: before the measurements, leaves were dark-adapted for 30 min by using special leaf clips, then the leaf samples were measured by *MINI-PAM* and the minimum fluorescence (F_0) and maximum fluorescence (F_m) were obtained. Instant light-response curves were obtained using the light-curve programmer of the *MINI-PAM*, by setting the intensity of actinic illumination as 1 s, and the duration 40 s. PAR values ranged as 0, 105, 237, 349, 553, 796; 1,129 µmol(photon) m^{-2} s^{-1}; the steady-state fluorescence (F_s) and maximal fluorescence from light-adapted samples (F_m') were measured under each PAR. According to the study of Kramer *et al*. (2004), Y_{II}, q_L, Y_{NO}, Y_{NPQ}, and F_v/F_m were calculated as follows: $Y_{II} = (F_m' - F_s)/F_m'$, $q_L = F_0'(F_m' - F_s)/F_s(F_m' - F_0')$, $Y_{NO} = 1/[NPQ + 1 + q_L(F_m/F_0 - 1)]$, $Y_{NPQ} = 1 - Y_{II} - Y_{NO}$, and $F_v/F_m = (F_m - F_0)/F_m$.

Data analysis: The *R-studio* was used to perform the one-way analysis of variance (*ANOVA*) and *Duncan*'s multiple range test (*DMRT*) to determine the significant difference between treatments at 0.05 probability level. The gray association grade analysis was used to develop the relationships between P_N, F_v/F_m, BCF_{leaf}, and TF_{leaf} and leaf biomass.

Results

Chl *a* fluorescence: The q_L and Y_{II} were significantly affected by Pb and Zn stress (Figs. 1, 2). After 15 d of the treatment, the values of q_L and Y_{II} decreased with increasing of PAR intensity under all Pb and Zn treatments in the two studied plant species, respectively. The order of these two parameters decreased as CK > L1 > L2 > L3 at the same PAR intensity for the two species. The q_L and Y_{II} were significantly higher in *Z. schneideriana* than that in *K. paniculata* under corresponding Pb and Zn treatments. In addition, q_L and Y_{II} were significantly lower under Zn treatment compared to Pb treatment in the two plant species (Figs. 1, 2).

The Y_{NPQ} increased with increasing PAR under all Pb and Zn treatments for both plant species after 15 d of the treatment (Fig. 3). The Y_{NPQ} decreased in order: L3 > L2 > L1 > CK for the species under these heavy metal treatments, except in the *K. paniculata* under Zn treatments, the Y_{NPQ} was higher in control than that in L1 and L2 treatments when PAR intensity was over 553 µmol(photon) m^{-2} s^{-1} (Fig. 3*C*). Although Pb treatments resulted in increases of Y_{NO} for *K. paniculata* and *Z. schneideriana* under PAR intensities when compared with the control, no significant differences of Y_{NO} were found between these Pb treatments (Fig. 4). No significant differences of Y_{NPQ} were found under the same Pb treatment for these two plant species. The Y_{NO} under Pb treatments was obviously higher in *K. paniculata* than that of *Z. schneideriana.* The Y_{NPQ} was significantly higher under Pb treatment compared to Zn treatment for the same tested plant in species. In contrast, the Y_{NO} was significantly lower under Pb treatment compared to Zn treatment (Figs. 3, 4).

Maximum net photosynthetic rate and maximum quantum efficiency: The P_N and F_v/F_m decreased significantly in both Pb and Zn treatments compared with the control (CK), except of the value of F_v/F_m, where no significant differences were found between the L1, L2, and control treatments (Table 1). The P_N and F_v/F_m were higher in *Z. schneideriana* than that in *K. paniculata* under Pb and Zn treatments, but significant differences were only detected in Zn treatment groups. The P_N and F_v/F_m values of *K. paniculata* and *Z. schneideriana* were significantly lower after Zn treatments than after Pb treatments.

Biomass production: The biomass of roots, stems, and leaves of *K. paniculata* and *Z. schneideriana* was significantly reduced under Pb and Zn treatments compared with the control after 15 d of treatment (Fig. 5), except for the roots and leaves of *K. paniculata*, where no significant differences were found under Pb treatments (Fig. 5). Specifically, the biomass of roots, stems, and leaves of *K. paniculata* decreased by 47.3–64.9, 57.6–78.0, and 56.7–83.3% under three concentrations of Pb compared to control, respectively. Similarly, the biomass of roots, stems, and leaves of *Z. schneideriana* decreased by 37.2–53.5, 16.7–48.9, and 32.3–75.3% compared to control. The biomass of roots, stems, and leaves of *K. paniculata* was reduced by 68.2–91.0, 73.8–89.5, and 66.2–92.9% under

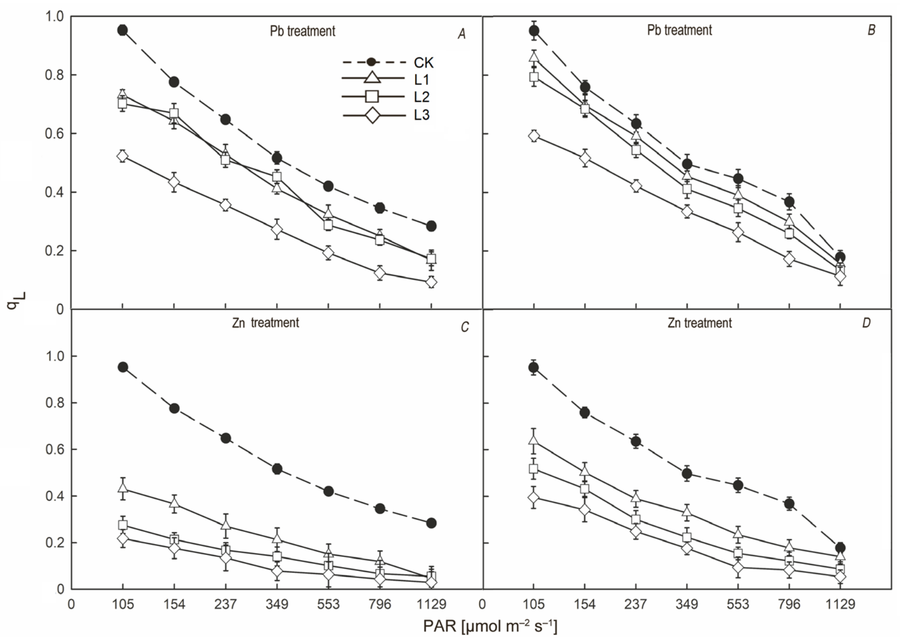

Fig. 1. Changes in the photochemical quenching (q_L) of *Koelreuteria paniculata* (*A*,*C*) and *Zelkova schneideriana* (*B*,*D*) leaves with different PAR intensities under four Pb and Zn treatments. CK (control), L1, L2, and L3 represent 0, 500, 600, and 900 mg kg^{-1}, respectively, of Pb or Zn in soil. Values are means ± SE, *n* = 6.

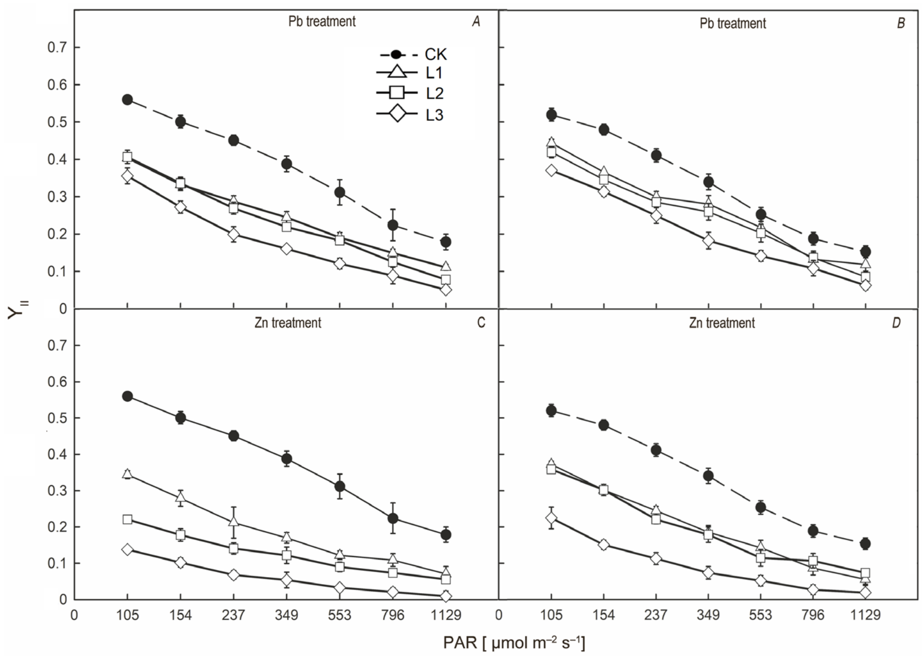

Fig. 2. Changes in the quantum efficiency of PSII (Y_{II}) of *Koelreuteria paniculata* (*A*,*C*) and *Zelkova schneideriana* (*B*,*D*) leaves with different PAR intensities under four Pb and Zn treatments. CK (control), L1, L2, and L3 represent 0, 500, 600, and 900 mg kg^{-1} of Pb or Zn, respectively, in soil. Values are means ± SE, *n* = 6.

three Zn treatments compared to control, respectively, while the corresponding values were 51.9–81.0, 53.7–74.7, and 69.5–88.7% in *Z. schneideriana*.

Concentrations, bioconcentration factor, and translocation factor: Under Pb and Zn treatments, the concentrations of Pb and Zn significantly increased with increasing contents in all organs of the tested plants compared to the control (Table 2). Pb was mainly accumulated in roots, then in stems, and the lowest amount was found in leaves. The Pb concentrations in different plant organs were higher in *K. paniculata* than those in *Z. schneideriana*. The concentrations of Zn were found similar in both stems and leaves of the tested plants. The Zn concentration in stems and leaves were higher in *K. paniculata* than that of *Z. schneideriana*. Plants accumulated more Zn than Pb in their stems and leaves.

Under Pb and Zn treatments, the BCF values of two plants were lower than that in the control (expect BCF_{root} of *Z. schneideriana* in Pb treatments), but the TF values were lower than control only in Pb treatments. BCF was higher in root (BCF_{root}) than in both stem (BCF_{stem}) and leaf (BCF_{leaf}) under Pb treatments for the two tested plants. The TF values were lower in Pb treatments than in Zn

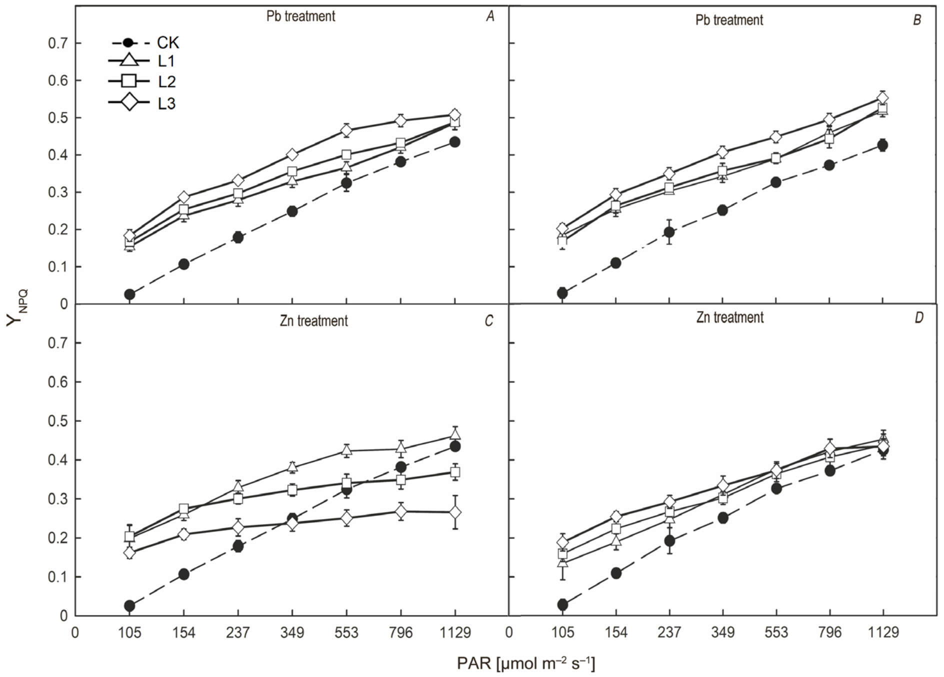

Fig. 3. Changes in the quantum yield of regulated energy dissipation (Y_{NPQ}) of *Koelreuteria paniculata* (*A*,*C*) and *Zelkova schneideriana* (*B*,*D*) leaves with different PAR intensities under four Pb and Zn treatments. CK (control), L1, L2, and L3 represent 0, 500, 600, and 900 mg kg^{-1} of Pb or Zn, respectively, in soil. Values are means ± SE, *n* = 6.

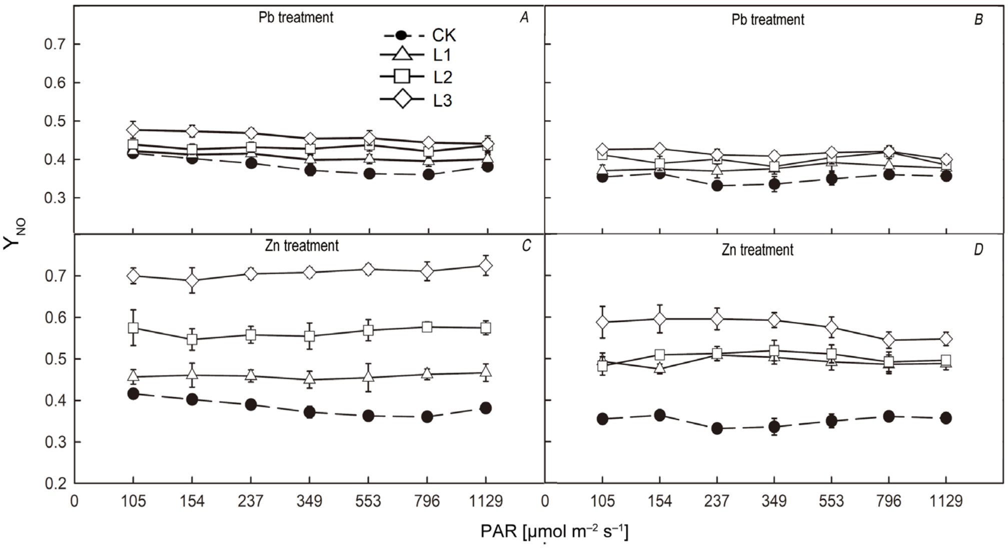

Fig. 4. Changes in the quantum yield of nonregulated energy dissipation (Y_{NO}) of *Koelreuteria paniculata* (*A*,*C*) and *Zelkova schneideriana* (*B*,*D*) leaves with different PAR intensities under four Pb and Zn treatments. CK (control), L1, L2, and L3 represent 0, 500, 600, and 900 mg kg^{-1} of Pb or Zn, respectively, in soil. Values are means ± SE, *n* = 6.

treatments for both *K. paniculata* and *Z. schneideriana*. The BCF values were proximate in different organs, but the TF values were much higher under Zn treatments. Meanwhile, the TF values of *K. paniculata* exceeded *Z. schneideriana*. The BCF_{stem}, BCF_{leaf}, and TF values were relatively high when the tested plants were treated by Zn.

Relationships of P_N, F_v/F_m, BCF_{leaf} and TF_{leaf} to leaf biomass: Leaf biomass productions of *K. paniculata* and *Z. schneideriana* were related to various selected Chl fluorescence parameters and heavy metal accumulation coefficients at different levels (Table 3). Under Pb stress, leaf biomass production of the tested plants was more closely related to P_N and F_v/F_m than to BCF_{leaf} and TF_{leaf}. On the contrary, leaf biomass production was more affected by BCF_{leaf} and TF_{leaf} than P_N and F_v/F_m under Zn treatments for the examined plant species of *K. paniculata* and *Z. schneideriana*.

Discussion

In the present study, we found that Pb and Zn stress resulted in a significant reduction of q_L and Y_{II} and an increase of Y_{NPQ} and Y_{NO} in *K. paniculata* and *Z. schneideriana*. The

Table 1. Response of the maximum quantum use efficiency (F_v/F_m) and the maximum net photosynthetic rate (P_N) in the leaves of *Koelreuteria paniculata* and *Zelkova schneideriana* to Pb and Zn stress. The data represent mean ± SE, the values followed by *different capital letters* within a line represent significant difference at level of 0.05 between plant species; *different small letters* within a column indicate significant difference at level of 0.05 under the different Pb or Zn treatment gradient. CK (control), L1, L2, and L3 represent 0, 500, 600, and 900 mg kg^{-1}, respectively, of Pb or Zn in soil.

Test set	Treatment	P_N [μmol(CO_2) m^{-2} s^{-1}]		F_v/F_m	
		K. paniculata	*Z. schneideriana*	*K. paniculata*	*Z. schneideriana*
Pb	CK	7.51 ± 0.09^{Aa}	8.01 ± 0.04^{Aa}	0.81 ± 0.08^{Aa}	0.84 ± 0.03^{Aa}
	L1	5.92 ± 0.12^{Ab}	6.21 ± 0.08^{Ab}	0.73 ± 0.06^{Aa}	0.77 ± 0.10^{Aa}
	L2	4.57 ± 0.11^{Ac}	5.33 ± 0.11^{Ac}	0.65 ± 0.08^{Aa}	0.72 ± 0.08^{Aa}
	L3	3.51 ± 0.15^{Ad}	4.14 ± 0.13^{Bd}	0.57 ± 0.09^{Ab}	0.64 ± 0.09^{Ab}
Zn	CK	7.51 ± 0.09^{Aa}	8.01 ± 0.04^{Aa}	0.81 ± 0.08^{Aa}	0.84 ± 0.03^{Aa}
	L1	3.73 ± 0.33^{Ab}	4.45 ± 0.05^{Bb}	0.42 ± 0.11^{Ab}	0.58 ± 0.08^{Bb}
	L2	2.48 ± 0.27^{Ac}	3.23 ± 0.21^{Bc}	0.31 ± 0.12^{Ac}	0.55 ± 0.16^{Bb}
	L3	1.70 ± 0.13^{Ad}	2.05 ± 0.10^{Bd}	0.22 ± 0.09^{Ad}	0.32 ± 0.10^{Bc}

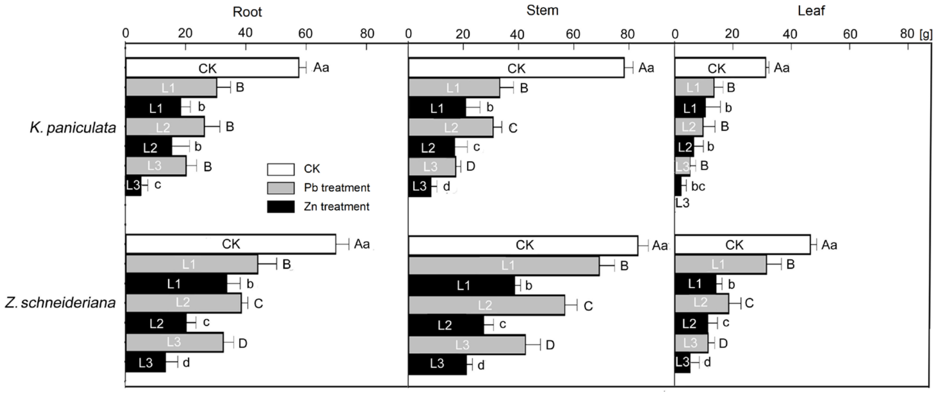

Fig. 5. Distribution of root, stem, and leaf biomass of *Koelreuteria paniculata* and *Zelkova schnei-deriana* under four Pb and Zn treatments. CK (control), L1, L2, and L3 represent 0, 500, 600, and 900 mg kg^{-1} of Pb or Zn, respec-tively, in soil. *Different capital letters* beside the columns indicate the significant differences at level of 0.05 between different Pb treatments; *different small letters* beside the columns indicate the significant differences at level of 0.05 between different Zn treatments. Values are means of $n = 6$, bar indicates standard error.

negative effects of Pb and Zn on these photosynthetic parameters were stronger with the increasing Pb and Zn concentrations (Figs. 1–4, Table 3). The reduction of q_L and Y_{II} implied that the open fraction of PSII reaction center declined, the efficiency of electron transport was reduced, which finally resulted in a reduction of P_N of *K. paniculata* and *Z. schneideriana* under Pb and Zn stress (Table 1). The results were in line with findings from previous studies (Rapacz 2002, Kramer *et al*. 2004). For example, Enami *et al*. (1994) reported that the reaction center of PSII of spinach suffered reversible inactivation or irreversible damage under heavy metal stress. Ye *et al*. (2014) found that environmental stress blocked photosynthetic primary reaction and reduced the efficiency of the original light energy conversion for *Broussonetia papyrifera* young plants. It was reported that the reduction of q_L and Y_{II} usually led to a decrease of open fraction of PSII reaction centers and efficiency of electron transport which blocked synthesis of ATP and NADPH and caused a reduction of plant carbon fixation and assimilation efficiency (Szarek and Ting 1974). In addition, the function of the D1 protein was easily impaired under stress conditions (Bricker and Frankel 2002, Khatoon *et al*. 2009, Cheng *et al*. 2016, Xue *et al.* 2017), which led to inhibition of PSII electron transport rate what corresponded to the reduction of Y_{II} and q_L of the tested plants under different Pb treatments.

F_v/F_m is considered as a sensitive indicator for describing the capacity of photosynthetic apparatus to perform photosynthesis (Mlinarić *et al*. 2017). Our study showed that under Pb and Zn treatments the F_v/F_m was significantly lower than in the control (Table 1), indicating the damage of PSII under heavy metal stress (Prieto *et al*. 2009, Bayçu *et al*. 2017). The reduction of F_v/F_m could be related to several alterations or damages at the structural and functional levels of the photosynthetic apparatus (Prasad 2003). Plants might produce relatively large amount of reactive oxygen species (ROS) under metal stress resulting in oxidative stress, which impairs membrane integrity and causes a reduction of F_v/F_m (Foyer and Noctor 2000, Takahashi and Murata 2008, de Silva

Table 2. Pb and Zn accumulation concentration, bioconcentration factor (BCF), and translocation factor (TF) of different organs of *Koelreuteria paniculata* and *Zelkova schneideriana.* The data represent mean ± SE. Values followed by *different capital letters* within a column are significantly different at 0.05 level under the different gradient; *different small letters* within a line represent significant difference at level of 0.05 between different plant organs. CK (control), L1, L2, and L3 represent 0, 500, 600, and 900 mg kg^{-1}, respectively, of Pb or Zn in soil.

	Treatment	Accumulation concentration [mg kg^{-1}]			BCF values			TF values	
		Root	Stem	Leaf	BCF$_{root}$	BCF$_{stem}$	BCF$_{leaf}$	TF$_{stem/root}$	TF$_{leaf/root}$
Pb treatment									
K. paniculata	CK	15.2 ± 0.8^{Aa}	5.7 ± 0.3^{Ab}	7.0 ± 0.4^{Ab}	0.75^{Aa}	0.30^{Ab}	0.35^{Ab}	0.40^{Aa}	0.47^{Aa}
	L1	220.8 ± 3.6^{Ba}	38.4 ± 1.8^{Bb}	30.2 ± 2.6^{Bc}	0.44^{Ba}	0.08^{Bb}	0.06^{Bb}	0.17^{Ba}	0.14^{Ba}
	L2	243.1 ± 2.9^{Ca}	43.1 ± 3.7^{Cb}	31.7 ± 1.7^{Cc}	0.37^{Ba}	0.07^{Bb}	0.05^{Bb}	0.18^{Ba}	0.13^{Ba}
	L3	298.7 ± 5.7^{Da}	53.7 ± 2.6^{Db}	36.8 ± 3.2^{Dc}	0.29^{Ba}	0.05^{Bb}	0.04^{Bb}	0.18^{Ba}	0.12^{Ba}
Z. schneideriana	CK	4.6 ± 0.2^{Aa}	4.1 ± 0.6^{Aa}	7.3 ± 0.4^{Aa}	0.25^{Aa}	0.20^{Aa}	0.35^{Ab}	0.80^{Aa}	1.40^{Ab}
	L1	147.1 ± 4.8^{Ba}	25.4 ± 4.2^{Bb}	23.6 ± 0.9^{Bb}	0.29^{Aa}	0.05^{Bb}	0.05^{Bb}	0.17^{Ba}	0.16^{Ba}
	L2	199.3 ± 6.1^{Ca}	35.2 ± 1.1^{Cb}	26.5 ± 1.9^{Bb}	0.33^{Aa}	0.06^{Bb}	0.05^{Bb}	0.18^{Ba}	0.14^{Ba}
	L3	244.5 ± 3.9^{Da}	39.9 ± 0.8^{Ca}	38.8 ± 2.4^{Cb}	0.27^{Aa}	0.04^{Ba}	0.04^{Bb}	0.16^{Ba}	0.16^{Ba}
Zn treatment									
K. paniculata	CK	33.7 ± 2.1^{Aa}	32.8 ± 0.7^{Aa}	39.7 ± 1.8^{Ab}	1.17^{Aa}	1.10^{Aa}	1.33^{Ab}	0.97^{Aa}	1.18^{Ab}
	L1	155.2 ± 4.4^{Ba}	130.5 ± 2.9^{Bb}	120.6 ± 3.7^{Bc}	0.31^{Ba}	0.26^{Ba}	0.24^{Ba}	0.85^{Ba}	0.78^{Bb}
	L2	132.9 ± 1.7^{Ca}	143.2 ± 4.7^{Ba}	154.1 ± 2.1^{Ca}	0.22^{Ba}	0.24^{Ba}	0.23^{Ba}	1.08^{Ba}	1.02^{Ca}
	L3	123.6 ± 6.3^{Da}	216.1 ± 3.1^{Cb}	202.2 ± 1.1^{Dc}	0.14^{Ca}	0.24^{Bb}	0.22^{Bb}	1.74^{Ca}	1.63^{Da}
Z. schneideriana	CK	39.1 ± 2.2^{Aa}	16.4 ± 1.7^{Ab}	33.9 ± 2.5^{Aa}	1.30^{Aa}	0.53^{Ab}	1.13^{Ac}	0.41^{Aa}	1.13^{Ab}
	L1	104.3 ± 5.4^{Ba}	100.2 ± 1.8^{Bb}	90.8 ± 3.3^{Bb}	0.21^{Ba}	0.20^{Bb}	0.18^{Bb}	0.96^{Ba}	0.88^{Ba}
	L2	118.7 ± 2.9^{Ca}	97.1 ± 4.4^{Cb}	108.2 ± 4.2^{Cc}	0.20^{Ba}	0.18^{Ba}	0.19^{Ba}	0.82^{Ba}	0.91^{Ca}
	L3	147.6 ± 3.6^{Ca}	122.6 ± 2.8^{Da}	121.8 ± 2.8^{Da}	0.16^{Ca}	0.14^{Ca}	0.14^{Ca}	0.83^{Ba}	0.82^{Ba}

Table 3. Associational grade and rank between leaf biomass and maximum net photosynthetic rate (P_N), maximum quantum use efficiency (F_v/F_m), bioconcentration factor (BCF$_{leaf}$), and translocation factor (TF$_{leaf}$) in *Koelreuteria paniculata* and *Zelkova schneideriana* plants under Pb and Zn treatment. L1, L2, and L3 represent 500, 600, and 900 mg kg^{-1}, respectively, of Pb or Zn in soil.

Parameter	Treatment	Pb treatment				Zn treatment			
		K. paniculata	Rank	*Z. schneideriana*	Rank	*K. paniculata*	Rank	*Z. schneideriana*	Rank
P_N	L1	0.730	4	0.823	3	0.703	12	0.592	10
	L2	0.746	3	0.700	5	0.892	11	0.649	8
	L3	0.918	1	0.966	1	1.181	7	0.672	7
F_v/F_m	L1	0.452	10	0.473	4	0.977	10	0.493	12
	L2	0.603	6	0.819	6	1.085	9	0.559	11
	L3	0.750	2	0.838	2	1.161	8	0.642	9
BCF$_{leaf}$	L1	0.727	5	0.466	12	1.340	3	0.684	6
	L2	0.586	8	0.600	8	1.348	2	0.719	5
	L3	0.441	11	0.611	10	1.361	1	0.799	4
TF$_{leaf}$	L1	0.442	12	0.467	11	1.290	4	0.803	3
	L2	0.589	7	0.602	7	1.247	6	0.808	2
	L3	0.448	9	0.536	9	1.251	5	0.839	1

et al. 2012). Therefore, photosynthesis was inhibited and this led to the decrease of the efficiency of light energy utilization. The reduction of plant biomass in this experiment indirectly reflected the damage of PSII and the inhibition of photosynthesis.

It is worthy to note that although the two plant species experienced similar concentrations of Pb and Zn, their stress tolerances were different. Under Pb and Zn treatments, the photoprotective mechanisms of the plants started as demonstrated by the increase of both Y_{NPQ} and Y_{NO} in the treated groups compared to the control groups (Figs. 3, 4). The change patterns of Y_{NPQ} were similar for the two plant species under the same Pb treatment, but Y_{NO} was obviously higher in *K. paniculata* than in *Z. schneideriana*.

This indicates *Z. schneideriana* exhibited strong Pb-stress tolerance due to its strong photoprotective mechanism and slower physiological decline. Similarly, under the same Zn treatment, the stress tolerance was slightly higher in *Z. schneideriana* than that in *K. paniculata*. The results were consistent with findings from previous studies for drought and saline stress (Yuan *et al*. 2014, Yang *et al*. 2016). Comparing the effects of Pb and Zn on *K. paniculata* and *Z. schneideriana*, we obtained that under the same concentration of Pb and Zn, the toxicity of Zn on Chl fluorescence and plant biomass production was higher than that of Pb. The reason might be that Zn is more easily transported to the leaves than Pb and the accumulation of Zn in leaves was higher than that of Pb in leaves (Table 2).

The damage mechanisms responsible for the inhibition of the photosystems could be different due to the variation of translocation and accumulation of the two heavy metals in plants. In the present study, Pb was mainly accumulated in roots of both plants (Table 2), implying that this metal was limited to the apoplastic space of the cortex and its loading into the vascular cylinder was effectively stopped by the endodermal Casparian strips of the root. Thus, Pb was often found to be accumulated in or beyond the endodermis (Jones *et al*. 1973, Ignatius *et al*. 2014). Our results were in agreement with previous studies (Michalak and Wierzbicka 1998, Antosiewicz *et al*. 2003, Sharma and Dubey 2005). At the same time, the endodermis of root only partially prevented the movement of Pb from root to stem (Verma and Dubey 2003), which resulted in a small amount of Pb entering the stems and then being translocated to leaves. The result supported our first hypothesis that as a nonessential element for plant growth and development, Pb would be transported less to plant leaves than Zn. And of four parameters in our study, the effect of Pb stress on plant biomass production was more related to photosynthesis than related to $\mathrm{BCF_{leaf}}$ and $\mathrm{TF_{leaf}}$ (Table 3).

In contrast, Zn was easily transformed and accumulated in stems and leaves compared to Pb (Table 2). Interestingly, changes in leaf biomass of the two examined species were more affected by translocation and bioconcentration parameters (such as $\mathrm{BCF_{leaf}}$ and $\mathrm{TF_{leaf}}$) than by Chl fluorescence parameters (such as P_N and $\mathrm{F_v/F_m}$) (Table 1). The results indicated that the accumulated Zn in leaves had primary contribution to phytotoxic effects. Bernardini *et al.* (2016) observed a similar phenomenon where Zn was accumulated in *Phragmites australis* which affected plant photosynthesis. The increasing accumulation of Zn in plant leaves may be attributed to the inability of these two plant species to chelate Zn with organic and inorganic acids to make it insoluble and limit its transport from roots to stems and leaves (Jiang and Wang 2008). Accumulated Zn could affect the structure of the thylakoid membranes in chloroplasts and lead to a reduction of electron transport rates. Moreover, the inactivation of Chl *a* due to the replacement of $\mathrm{Mg^{2+}}$ by $\mathrm{Zn^{2+}}$ at the site of water photolysis might influence oxygen release process (Santos *et al*. 2014). Therefore, Zn stress on plant growth and biomass production was directly related to the accumulation of Zn in leaves at first and then reduced P_N and photosynthesis. Our results showed leaf biomass production was more affected by $\mathrm{BCF_{leaf}}$ and $\mathrm{TF_{leaf}}$ than P_N and $\mathrm{F_v/F_m}$ under Zn treatments (Table 3, Fig. 5). This is not only supporting our conclusion mentioned above, but also supports our second hypothesis that Zn could be largely absorbed, transported, and accumulated in leaves compared to Pb, which might result in more serious damage in photosynthetic performance.

Conclusion: Pb and Zn stress significantly affected the photosynthetic process of *K. paniculata* and *Z. schneideriana* by disturbing energy balance and allocation in PSII function. It seems that the stress resistance of Pb and Zn was higher in *Z. schneideriana* than that in *K. paniculata*. Due to limitation of transport, Pb was mainly accumulated in plant roots, but the inhibition of photosynthesis by Pb stress had a high associational grade and ranked with biomass production. On the contrary, Zn was largely accumulated in leaves because this metal was easily transported. Thus, Zn stress on plant growth and biomass production was directly related to the accumulation of Zn in leaves in which excess Zn would damage chloroplast functioning.

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