Acta Geochim (2016) 35(3):309–315
DOI 10.1007/s11631-016-0099-1

ORIGINAL ARTICLE

Photosynthetic capability and Fe, Mn, Cu, and Zn contents in two Moraceae species under different phosphorus levels

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Received: 8 December 2015 / Revised: 16 January 2016 / Accepted: 21 February 2016 / Published online: 27 February 2016

Abstract The strong adaptability of *Broussonetia papyrifera* (L.) Vent. to low phosphorus (P) conditions can be attributed to the large amount of root-exuded organic acids and the high efficiency of P extraction. However, microelement contents are influenced by low-P stress, and their effects on the photosynthetic capability of *B. papyrifera* remain unknown. In this study, we investigated the effects of low-P treatment on net photosynthetic rate (P_N); chlorophyll *a* fluorescence (ChlF) characteristics; and Fe, Mn, Cu, and Zn contents of *B. papyrifera* and *Morus alba* L. seedlings. Results show that *B. papyrifera* exhibited better photosynthetic capability under moderate P deficiency (0.125, 0.063, and 0.031 mmol/L P treatments), whereas the photosynthetic capability of *M. alba* decreased under moderate and severe P deficiency (0.016 and 0 mmol/L P treatments). Under moderate P deficiency, the decrease in Cu and Zn contents in *B. papyrifera* was lower than that in *M. alba*. Under severe P deficiency, a considerable decrease of photosynthetic capability in *B. papyrifera* and *M. alba* was associated with low Cu and Zn contents. The P_N of the two Moraceae species exhibited a better correlation with Cu and Zn contents than with Fe or Mn content. P deficiency could not only decrease cyclic photophorylation and photosynthetic efficiency, but could also affect the stability of thylakoid membrane structure and electron transport efficiency by influencing the contents of Cu or Zn, thereby affecting photosynthesis.

Keywords Adaptability · Chlorophyll *a* fluorescence · Microelement · Organic acids · Sensitive

Abbreviations

Φ_{PSII}	Actual photochemical quantum efficiency of PSII
B. papyrifera	*Broussonetia papyrifera* (L.) Vent
ChlF	Chlorophyll *a* fluorescence
F_s	Fluorescence in stable state
F_o	Initial fluorescence
LSD	Least significant difference
F_m	Maximum fluorescence
F'_m	Maximum fluorescence in the light-adapted state
F_v/F_m	Maximum quantum yield of PSII
M. alba	*Morus alba* L
P_N	Net photosynthetic rate
P	Phosphorus
PSII	Photosystem II
SE	Standard errors
F_v	Variable fluorescence

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1 Introduction

Broussonetia papyrifera (L.) Vent. and *Morus alba* L. are perennial tree species belonging to the family Moraceae and are characterized by higher growth rate and greater adaptability to adverse environments than other species in this family (Zhao et al. 2005). *B. papyrifera* is more tolerant to a low-phosphorus (P) environment (Liu et al. 2010).Unlike *M. alba*, *B. papyrifera* can acclimate to karst soil and resist alien invasion (Wu et al. 2009). A higher amount of organic acids is found in root exudates of *B. papyrifera* than in *M. alba* in low-P environments (Shahbaz et al. 2006). Root-exuded organic acids sometimes form organometallic complexes with insoluble phosphoric compounds in soil, releasing available P (Jones and Darrah 1994); the strong adaptability of *B. papyrifera* to low-P environments can be attributed to the high efficiency of P extraction (Zhao and Wu 2014). However, the root-exuded organic acids might also improve the bioavailability of microelements (Hoffland et al. 1992).The concentration and uptake of plant microelements increase when smaller amounts of P are applied (Racz and Haluschak 1974; Rutkowska et al. 2014). Nonetheless, the relationship between the increase in concentration of plant microelements and the adaptability of *B. papyrifera* remains unknown.

Inorganic P is one of the least available nutrients in the soils of several terrestrial ecosystems (Alloush et al. 2003; Li et al. 2006). P deficiency leads to a considerable decrease in cyclic photophorylation and photosynthetic efficiency (Watanabe and Yoshida 1970). Some studies have demonstrated that P deficiency induces possible photoinhibition and damage to photosystem II (PSII) (Li et al. 2004). Moreover, the uptake of microelements—such as Fe, Mn, Cu, and Zn—in plants is also related to photosynthesis. Fe is an essential micronutrient for plants (Hao et al. 2007). Bertamini et al. (2002) proved that a low photosynthetic electron transport rate in Fe-deficient grapevine leaves is mainly due to the loss of PSII activity. Mn plays an important role in the water-splitting reaction leading to oxygen evolution in photosynthesis (Sauer 1980). The most important role of Cu is associated with blocking of photosynthetic electron transport, leading to production of radicals which start peroxidative chain reactions involving membrane lipids (Fernandes and Henriques 1991). Finally, Zn deficiency causes reduction of electron use in dark reactions and decreases heat dissipation (Hajiboland et al. 2010).

A certain amount of supplemental P increases the uptake of some micronutrients, while decreasing the uptake of Zn in some plant organs (Nyoki and Ndakidemi 2014). The total amounts of Fe, Mn, Cu, and Zn absorbed by aboveground plant tissue decrease in treatments in which nutrient deficiencies are observed, but the micronutrient concentrations in tissues do not decrease (Choi and Lee 2012). Root-exuded organic acids might increase the uptake of microelements in plants, compensate for the loss of microelements under a low-P environment, and slow the decrease of microelement contents. As a result, the lower rate of decrease in microelement contents could alleviate the damage caused by microelement deficiency to plants in a low-P environment, thereby enhancing photosynthesis. Given that microelements play important roles in photosynthesis, the variations in microelement contents could be a photosynthetic adaptive mechanism of *B. papyrifera* to low-P stress.

Non-invasive methods such as chlorophyll *a* fluorescence (ChlF) have been used to observe various types of stress affecting the photosynthetic machinery (Huang et al. 2004). ChlF has been widely used to evaluate plant tolerance to environmental stresses (Gray et al. 2006). The present study examined net photosynthetic rate (P_N); ChlF parameters; and Fe, Mn, Cu, and Zn contents in two Moraceae species. The influence of Fe, Mn, Cu, and Zn contents on the photosynthetic capability of *B. papyrifera* and *M. alba* was analyzed. Results of this study provide deeper understanding of the photosynthetic adaptive mechanism of *B. papyrifera* in a low-P environment, which can be used as a guide for selecting appropriate plant species for reforestation efforts in a heterogeneous environment.

2 Materials and methods

2.1 Plant growth and low-P treatment

Seedlings of *B. papyrifera* and *M. alba* were cultivated and treated according to Xing and Wu (2014). After 90 days of growth, the nutrient solution was replaced by a modified Hoagland solution (Hoagland and Arnon 1950) containing 6 mmol/L KNO_3, 4 mmol/L$Ca(NO_3)_2$, 2 mmol/L $MgSO_4$, 2 mmol/L Fe(Na)EDTA, 2 µmol/LKCl, 50 µmol/L H_3BO_3, 4 µmol/L $MnSO_4$, 4 µmol/L $ZnSO_4$, 0.2 µmol/L $CuSO_4$, and 0.2 µmol/L $(NH_4)_6MO_7O_{24}$. Five low-P treatments of 0.125, 0.063, 0.031, 0.016, and 0 mmol/L were simulated by varying concentration combinations of $NH_4H_2PO_4$ and NH_4Cl; 0.250 mmol/L P was used as the control. Determination was conducted on day 45 from the onset of treatment. Five recently-matured leaves from each of the treated seedlings were measured.

2.2 Measurement of net photosynthetic rate

Net photosynthetic rate was determined using the method in Xing and Wu (2012).

2.3 Measurement of chlorophyll *a* fluorescence

ChlF was determined according to the method described by Xing and Wu (2012). The maximum quantum yield of PSII (F_v/F_m) was calculated as $(F_m - F_o)/F_m$, where $F_v = F_m - F_o$. The actual photochemical quantum efficiency of PSII (Φ_{PSII}) was calculated as $(F'_m - F_s)/F'_m$.

2.4 Contents of Fe, Mn, Cu, and Zn

Five plants from each treatment group were selected and dried in an oven at 80 °C. Approximately 0.3–0.5 g of dried plant tissue was digested using the H_2SO_4–H_2O_2 digestion method (Xu 2000).The Fe, Mn, Cu, and Zn contents were determined using atomic absorption spectroscopy (PE-5100-PC, PerkinElmer, USA).

2.5 Statistical analysis

All experimental measurements consisted of five replicates. Data were analyzed using SPSS software (version 13.0, SPSS Inc). The differences between low-P treatments were assessed using the least significant difference (LSD) post hoc test at a 5 % significance level ($p \leq 0.05$). Data were shown as the means ± standard errors (SE), which were determined using one-sample T test (confidence interval was 95 %). The correlation between P_N and content of Fe, Mn, Cu, or Zn was analyzed using bivariate correlations.

3 Results

3.1 Effect of low-P on net photosynthetic rate

M. alba showed a significant decrease in P_N from the onset of low-P treatment (Table 1). While the significant decrease of P_N of *B. papyrifera* appeared at 0.063 mmol/L. The P_N of *M. alba* exhibited a more significant decrease than that of *B. papyrifera* from 0.031 to 0.016 mmol/L. The values of P_N of *B. papyrifera* at 0.016 and 0 mmol/L were 49 % and 41 %, respectively, of the value of the control, while the values of P_N of *M. alba* at 0.016 and 0 mmol/L were only 38 % and 13 %, respectively, of the value of the control. The value of P_N of *B. papyrifera* was higher than *M. alba* at each low-P stress level.

3.2 Effects of low-P on ChlF parameters

The values of initial fluorescence (F_o) of *B. papyrifera* subjected to 0.016 and 0 mmol/L P treatments were higher than those in 0.250, 0.125, 0.063, and 0.031 mmol/L P treatments; the F_o values of *B. papyrifera* in treatments with P nutrient levels ranging from 0.250 to 0.031 mmol/L showed no significant difference (Fig. 1a). The F_o value of *M. alba* of the control was lower than that at other P nutrient levels; the F_o values of *M. alba* in treatments with P nutrient levels ranging from 0.125 to 0.016 mmol/L showed no significant difference.

The maximum quantum yields of PSII (F_v/F_m) of *B. papyrifera* at 0.016 and 0 mmol/L P treatments were lower than those of higher P treatments; the F_v/F_m values of *B. papyrifera* in treatments with P nutrient levels ranging from 0.250 to 0.031 mmol/L showed no significant difference (Fig. 1b). The F_v/F_m of *M. alba* of the control was higher than that of other P nutrient levels; the F_v/F_m values of *M. alba* in treatments with P nutrient levels ranging from 0.125 to 0.016 mmol/L showed no significant difference.

The actual photochemical quantum efficiencies of PSII (Φ_{PSII}) closely mimicked the pattern observed in maximum quantum yields. Φ_{PSII} values of *B. papyrifera* at 0.016 and 0 mmol/L were lower than those with higher P treatments; the Φ_{PSII} values of *B. papyrifera* in treatments with P nutrient levels ranging from 0.250 to 0.031 mmol/L showed no significant difference (Fig. 1c). The Φ_{PSII} of *M. alba* of the control was higher than of those subjected to P deficiency; the Φ_{PSII} values of *M. alba* in treatments with P nutrient levels ranging from 0.125 to 0.031 mmol/L showed no significant difference.

3.3 Effects of low-P on contents of Fe, Mn, Cu, and Zn

Fe, Mn, Cu, and Zn contents varied between plant species and P levels (Table 2). Low-P treatment was associated

Table 1 Effect of low-P on net photosynthetic rate

P nutrient level (mmol/L)	Photosynthetic rate, P_N (μmol/m^2 s)			
	B. papyrifera		*M. alba*	
	Mean ± SE	(%)[a]	Mean ± SE	(%)[a]
0.250	4.413 ± 0.112a	100	4.629 ± 0.212x	100
0.125	4.126 ± 0.328a	93	3.165 ± 0.351y	68
0.063	3.643 ± 0.114b	83	2.421 ± 0.264z	52
0.031	3.648 ± 0.135b	83	2.114 ± 0.183z	46
0.016	2.147 ± 0.423c	49	1.747 ± 0.096w	38
0.000	1.829 ± 0.236c	41	0.623 ± 0.158v	13

The mean ± SE ($n = 5$) is followed by different letters in the same column when values differ significantly—at $P \leq 0.05$, according to one-way ANOVA and *t* tests

[a] This column represents the percent value after low-P treatment with reference to that of the control plants

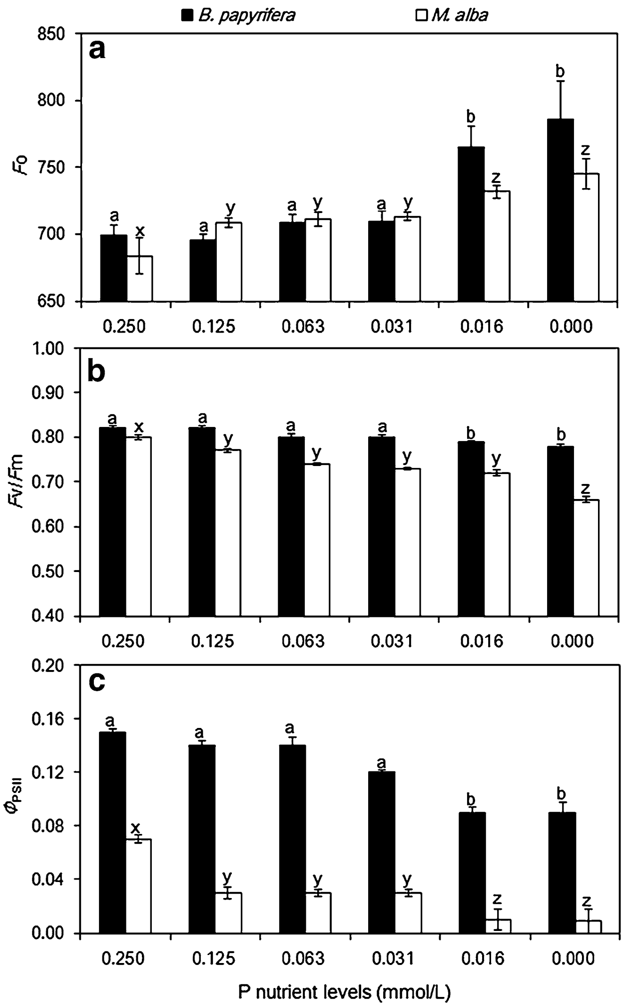

Fig. 1 Effects of low-P on initial fluorescence (F_o), maximum quantum yields of PSII (F_v/F_m) and the actual photochemical quantum efficiencies of PSII (Φ_{PSII}). **a** F_o; **b** F_v/F_m; **c** Φ_{PSII}. *Different letters* appear above the *error bars* of the same parameter of the same plant species when subsequent values differ significantly—at $P \leq 0.05$, according to one-way ANOVA and *t* tests

with lower contents of Fe and Mn at all P-deficient treatment levels in *B. papyrifera*, whereas the Fe and Mn contents in *M. alba* in treatments with P nutrient levels ranging from 0.250 to 0.031 mmol/L showed no significant difference. The micronutrient contents in *M. alba* in 0.016 and 0 mmol/L P treatments were lower than in higher P treatments.

Low-P treatment was consistently associated with lower contents of Cu in both *B. papyrifera* and *M. alba* (Table 2).

The contents of Zn in *B. papyrifera* in treatments with P nutrient levels ranging from 0.250 to 0.031 mmol/L showed no significant difference. The Zn contents of *B. papyrifera* at 0.016 and 0 mmol/L P treatments were lower than those higher-P treatments (Table 2).

3.4 Relationship between net photosynthetic rate and content of Fe, Mn, Cu, or Zn

The relationships between P_N and the content of Cu or Zn displayed good positive correlations (Fig. 2c, d), in which the determination coefficient (R^2) ranged from 0.245 to 0.865; the R^2 of Cu or Zn was greater than that of Fe or Mn (Fig. 2a, b). In other words, an increase in Cu and Zn contents correlated with an increase of P_N in both *B. papyrifera* and *M. alba*.

4 Discussion

Photosynthetic activity represents the growth potential of a plant (Walters et al. 1993). *B. papyrifera* exhibited better photosynthetic capability than *M. alba* under moderate P deficiency, whereas the photosynthetic capability of *M. alba* decreased significantly under moderate and severe P deficiency; the influence of low-P on photosynthesis was more severe in *M. alba* than in *B. papyrifera*. In addition, the resistances of *B. papyrifera* and *M. alba* to a low-P environment were different; the photochemical apparatus of *B. papyrifera* was not damaged under moderate P deficiency, whereas the increase of *Fo* in *B. papyrifera* under severe P deficiency indicated that the activity of PSII reaction centers had decreased. The response to decreased P of *Fv*/*Fm* and Φ_{PSII} in *B. papyrifera* also indicated little damage to the PSII reaction centers under moderate P deficiency. However, the activity of PSII reaction centers in *M. alba* decreased in low-P treatments; that is, the PSII reaction centers of *M. alba* were damaged under low-P stress conditions. When the P concentration of nutrient solution was higher than 0.031 mmol/L, the *B. papyrifera* exhibited good tolerance. However, the tolerance of *M. alba* decreased under even moderate P deficiency.

Under moderate P deficiency, the amount of root-exuded organic acids in *B. papyrifera* increased more significantly than in *M. alba* (Wu and Zhao 2013), and according to Hofland et al. (1992), the bioavailability of microelements around the root of *B. papyrifera* could be improved as a result. Due to the increase in root-exuded acids, the Cu content in *B. papyrifera* was higher than that in *M. alba*, and the Zn content in *B. papyrifera* exhibited a lower rate of decrease than that in *M. alba*. Since the most important role of Cu is associated with blocking of peroxidative chain reactions involving membrane lipids (Fernandes and Henriques 1991), higher Cu content in *B. papyrifera* could maintain the stability of thylakoid membrane structure more efficiently. Moreover, Zn could improve electron use in dark reactions (Hajiboland et al. 2010); therefore, the lower rate of decrease in Zn in *B. papyrifera* could maintain the stability of dark reactions more efficiently. By

Table 2 Effects of low-P on Fe, Mn, Cu, and Zn contents (mg/g)

Parameter	P nutrient level (mmol/L)	Parameter content (mg/g)			
		B. papyrifera		*M. alba*	
		Mean ± SE	(%)[a]	Mean ± SE	(%)[a]
Fe	0.250	0.118 ± 0.001a	100	0.098 ± 0.001x	100
	0.125	0.090 ± 0.000b	77	0.095 ± 0.001xy	97
	0.063	0.060 ± 0.000c	51	0.093 ± 0.000xy	95
	0.031	0.043 ± 0.000d	36	0.090 ± 0.000y	92
	0.016	0.038 ± 0.001e	32	0.015 ± 0.001z	15
	0.000	0.033 ± 0.000f	28	0.010 ± 0.001z	10
Mn	0.250	0.040 ± 0.000a	100	0.060 ± 0.001x	100
	0.125	0.030 ± 0.000b	75	0.058 ± 0.001x	97
	0.063	0.022 ± 0.000c	56	0.058 ± 0.002x	96
	0.031	0.018 ± 0.000d	44	0.055 ± 0.002x	92
	0.016	0.003 ± 0.000e	7	0.013 ± 0.001y	21
	0.000	0.003 ± 0.000e	6	0.003 ± 0.000z	4
Cu	0.250	0.045 ± 0.000a	100	0.040 ± 0.000x	100
	0.125	0.040 ± 0.001b	89	0.028 ± 0.000y	69
	0.063	0.033 ± 0.000c	72	0.023 ± 0.001z	56
	0.031	0.030 ± 0.000c	67	0.007 ± 0.000w	18
	0.016	0.003 ± 0.000d	7	0.005 ± 0.000w	13
	0.000	0.002 ± 0.000d	5	0.005 ± 0.000w	13
Zn	0.250	0.053 ± 0.001a	100	0.059 ± 0.000x	100
	0.125	0.050 ± 0.001ab	94	0.050 ± 0.001y	85
	0.063	0.048 ± 0.001b	89	0.048 ± 0.001y	80
	0.031	0.045 ± 0.000b	84	0.043 ± 0.000z	72
	0.016	0.015 ± 0.000c	28	0.008 ± 0.000w	13
	0.000	0.013 ± 0.000c	23	0.003 ± 0.000v	4

The mean ± SE ($n = 5$) is followed by different letters in the same column for the same parameter when values differ significantly—at $P \leq 0.05$, according to one-way ANOVA and t tests

[a] This column represents the percent value after low-P treatment with reference to that of the control plants

contrast, the damage caused by the decrease in Cu and Zn contents to *M. alba* could not be alleviated efficiently, and the photosynthesis of *M. alba* could not be meliorated. The results in the present study also indicate that the photosynthetic capability of *B. papyrifera* was relatively unaffected, whereas the photosynthetic capability of *M. alba* is sensitive to moderate P deficiency. Under severe P deficiency, the amount of root-exuded organic acids in *M. alba* increased more significantly than in *B. papyrifera* (Wu and Zhao 2013). Although the Cu content in *M. alba* exhibited a lower rate of decrease, the decrease in Zn content was significant. Under severe P deficiency, the increase in the amount of root-exuded organic acids in *B. papyrifera* and *M. alba* could not alleviate the loss of microelements. Moreover, a considerable decrease of photosynthetic capability in *B. papyrifera* and *M. alba* was associated with the lower Cu and Zn contents.

Given that the availability of Fe and Mn are higher than that of Cu or Zn in the soils of several terrestrial ecosystems(Chen et al. 2013), plant growth is more easily affected by Cu or Zn content in soil. In the present study, the applied amounts of Fe and Mn were probably enough for the growth of the two Moraceae species in low-P environments. P deficiency could not only bring about a decrease in cyclic photophorylation and photosynthetic efficiency(Watanabe and Yoshida 1970), but could also affect the stability of thylakoid membrane structure and electron transport efficiency by influencing the content of Cu or Zn, thereby affecting photosynthesis. Moreover, the P_N of the two Moraceae species exhibited a better correlation with Cu and Zn contents, rather than with Fe or Mn content. P deficiency had almost no effect on PSII activity or on the water-splitting reaction in either plant species.

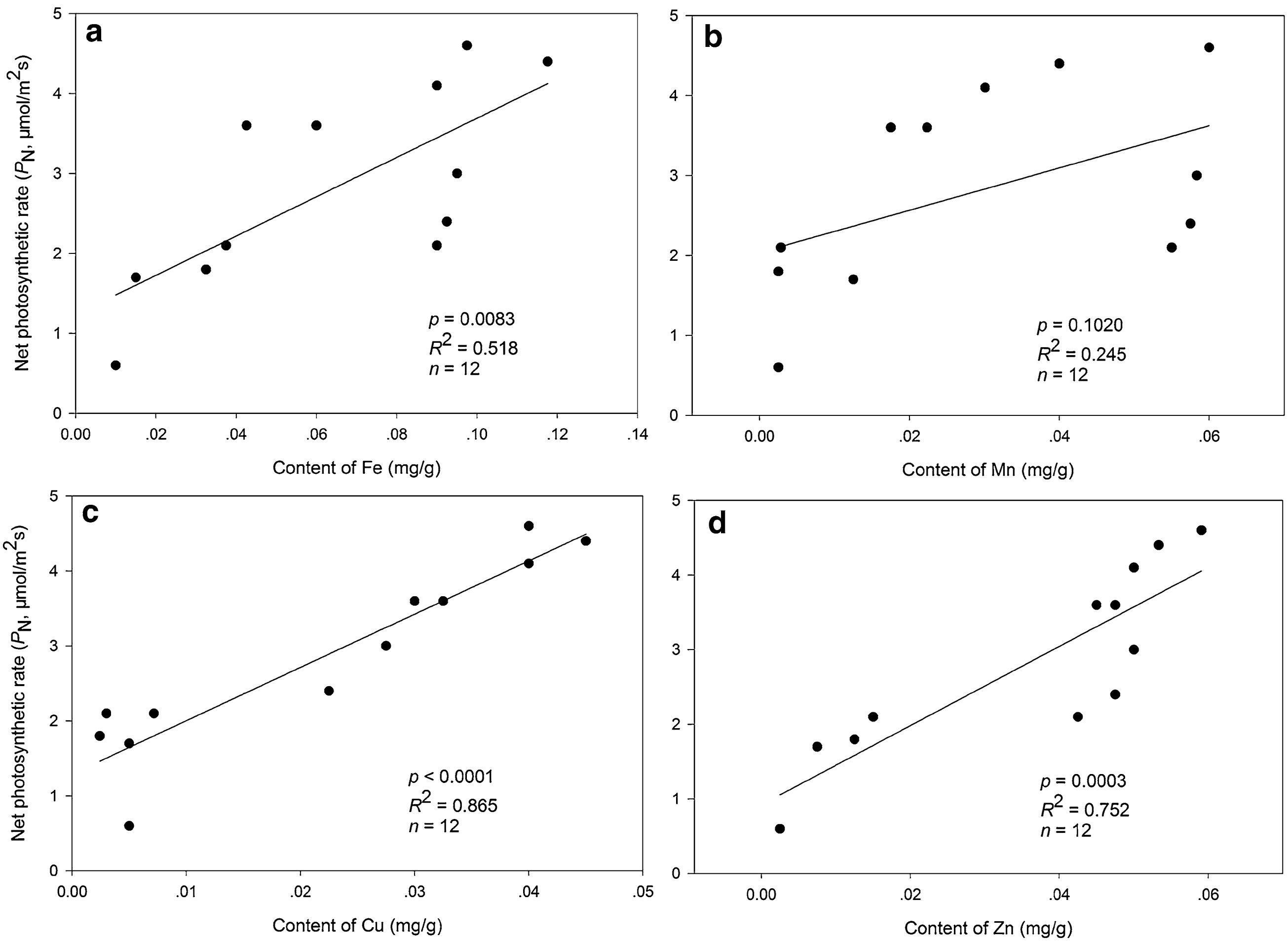

Fig. 2 Relationships between the net photosynthetic rate (P_N, μmol/m^2 s) and content of Fe, Mn, Cu, or Zn (mg/g). Note: *Y* is the P_N; *X* is the content of Fe, Mn, Cu or Zn. **a** Fe; **b** Mn; **c** Cu; **d** Zn

5 Conclusion

The responses of *B. papyrifera* and *M. alba* to low-P treatment with different Fe, Mn, Cu, and Zn contents varied in terms of photosynthetic capability. *B. papyrifera* exhibited better photosynthetic capability under moderate P deficiency, whereas the photosynthetic capability of *M. alba* decreased under moderate and severe P deficiency. Under moderate P deficiency, the decreases in Cu and Zn contents in *B. papyrifera* were lower than those in *M. alba*. Under severe P deficiency, a significant decrease of photosynthetic capability in *B. papyrifera* and *M. alba* was associated with lower Cu and Zn contents. The P_N of the two Moraceae species exhibited a better correlation with Cu and Zn contents than with Fe or Mn content. Furthermore, P deficiency could not only decrease the cyclic photophorylation and photosynthetic efficiency, but also affect the stability of thylakoid membrane structure and electron transport efficiency by influencing the content of Cu or Zn, thereby affecting photosynthesis. Nevertheless, P deficiency had almost no effect on PSII activity or water-splitting.

Acknowledgments This study was supported by the project of the National Natural Science Foundation of China (No. 31301243), a project funded by the Priority Academic Program Development of Jiangsu higher education institutions (PAPD), the research foundation for introduce talents of Jiangsu university (13JDG030), the brainstorm project on social development of Guizhou Province (SY[2010]3043).

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