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BRIEF COMMUNICATION

Changes in plant growth and photosynthetic performance of *Zizania latifolia* exposed to different phosphorus concentrations under hydroponic condition

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Abstract

The effects of phosphate concentration on plant growth and photosynthetic performance were examined in leaves of *Zizania latifolia*. Plants were grown for four weeks in a solution containing 0, 0.16, 0.64, and 2.56 mM orthophosphate. The results showed that the highest net photosynthetic rate (P_N) was achieved at 0.64 mM orthophosphate, which corresponded to the maximum content of organic phosphorus in leaves. Low phosphorus (low-P) content in the culture solution inhibited plant growth, affecting plant height, leaf length, leaf number, tiller number, and fresh mass of leaf, sheath, culm, root, and total plant. In addition, we observed that low-P (0.16 mM) did not hinder the growth of roots but increased the root:shoot ratio, and significantly decreased the chlorophyll content, P_N, stomatal conductance, and transpiration rate, but increased the intercellular CO_2 concentration. Additionally, low-P significantly decreased the maximum carboxylation rate of Rubisco, the maximum rate of ribulose-1,5-bisphosphate regeneration, the effective quantum yield of PSII photochemistry, photochemical quenching coefficient, and electron transport rate, but increased the nonphotochemical quenching. However, the maximal quantum yield of PSII photochemistry was not significantly affected by low-P. High phosphorus (2.56 mM) caused only a slight decrease in gas-exchange parameters. Therefore, the decrease in growth of P-deficient Z. *latifolia* plants could be attributed to the lowered photosynthetic rate.

Additional key words: chlorophyll *a* fluorescence; growth characteristics; phosphorus availability; photosynthesis.

Phosphorus (P) is an essential nutrient that is required for all major developmental processes in plants, and it also plays a pivotal role in energy conservation, metabolic regulation, and signal transduction cascade as it is essential constituent of compounds, such as ATP, nucleic acids, and phospholipids (Schachtman *et al*. 1998, Raghothama 1999). Photosynthesis is also one of the metabolic processes where P is involved in, because light reactions of photosynthesis form ATP from ADP and P_i (Foyer and Spencer 1986) and the formation of starch and sucrose relies on hexose phosphates and triose phosphates derived from the Calvin cycle (Linka and Weber 2010).

P deficiency is an important abiotic stress factor for crops, which can limit the global crop yield by 30–40% (Vance *et al*. 2003). Phosphate deficiency can restrict plant growth (Nichols *et al*. 1979, Jacob and Lawlor 1991, Silber *et al*. 2000) by reducing the P concentration in leaves (Jacob and Lawlor 1992, Schachtman *et al*. 1998, De Groot *et al*. 2001, Ghannoum and Conroy 2007), by an increase of acid phosphatase activity (Duff *et al*. 1994), or by lowering the solar radiation interception, thereby restricting the expansion of newly developed leaves (Radin

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Abbreviations: Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; ETR – electron transport rate; FM – fresh mass; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; J_{max} – maximum rate of RuBP regeneration; NPQ – nonphotochemical quenching; P – phosphorus; P_i – inorganic phosphorus; P_N – net photosynthetic rate; P_o – organic phosphorus; P_{tot} – total phosphorus; q_P – photochemical quenching coefficient; V_{cmax} – maximum carboxylation rate of Rubisco; Φ_{PSII} – effective quantum yield of PSII photochemistry.
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and Eidenbock 1984, Pieters *et al*. 2001, Chiera *et al*. 2002, De Groot *et al*. 2003).

Low-P treatment can induce significant reduction in shoot growth but not significant decrease in root growth in soybean (*Glycine max* Merr.) (Fredeen *et al*. 1989), and it greatly affects leaf area in sugar beet (Rao and Terry 1989). In addition, phosphate deficiency can also alter the normal pattern of tiller emergence and decrease the number of tillers in wheat (Rodríguez *et al*. 1999). P deficiency has been shown to inhibit photosynthesis in many crops, such as sugar beet (*Beta vulgaris* L.) (Terry and Ulrich 1973, Rao and Terry 1989), barley (*Hordeum vulgare* L.) (Foyer and Spencer 1986), soybean (*Glycine max*) (Fredeen *et al*. 1989, 1990), maize (*Zea mays* L.) (Usuda and Shimogawara 1991), sunflower (*Helianthus annuus* L.) (Plesničar *et al*. 1994), and tobacco (*Nicotiana tabacum* L.) (Pieters *et al*. 2001). P deficiency can also decrease light saturation point (Fredeen *et al*. 1989, Rao and Terry 1989, De Groot *et al*. 2003), and strongly affect carboxylation efficiency and the apparent quantum yield (Jacob and Lawlor 1991, 1992), resulting in a decrease in the maximum carboxylation rate of Rubisco (V_{cmax}) and maximum rates of RuBP regeneration (J_{max}) (Lewis *et al*. 1994, Loustau *et al*. 1999).

Low-P stress can decrease stomatal conductance (g_s) (Radin 1984, Rao and Terry 1989, Jacob and Lawlor 1991, Clarkson *et al*. 2000), reduce leaf water potential and electron transport rate (ETR) (Radin and Eidenbock 1984), and increase intercellular CO_2 concentration (C_i) (Fredeen *et al*. 1990, Jacob and Lawlor 1991). However, at higher P supply, P_N can decrease, thus resulting in P accumulation in plant cells (Shane *et al*. 2004). Under P deficiency, photoinhibition of photosynthesis is aggravated and non-radiate energy heat dissipation plays an important role against photodamage to the photosynthetic apparatus (Guo *et al*. 2003). Meanwhile, decrease in effective quantum yield of PSII photochemistry (Φ_{PSII}), photochemical quenching coefficient (q_P), and ETR, and increase in non-photochemical quenching (NPQ) occurs (Van Kooten and Snel 1990, Plesničar *et al*. 1994, Li *et al*. 2004).

As one of the important aquatic vegetables in China, *Zizania latifolia* Turcz. is traditionally cultivated for its swollen culm (Zhang *et al*. 2012, Yan *et al*. 2013a). The yield of this crop is determined to a great extent by the number of tillers that form swollen culms. Application of P fertilizers can significantly increase the yield and improve quality of *Z. latifolia* because the initiation and subsequent performance of tillers is affected by P (Rodríguez *et al*. 1999, Jiang *et al*. 2003). However, to our knowledge, there are no data on the effect of different concentrations of P on the gas-exchange characteristics and chlorophyll (Chl) *a* fluorescence of *Z. latifolia*, and relationship between P and photosynthesis is not clear in this species. The objective of the present study was to evaluate the effects of phosphate concentrations under hydroponic condition on plant growth, photosynthetic gas exchange, and Chl *a* fluorescence in leaves of the crop.

Sixteen clusters of *Z. latifolia* (cv. Zhejiao No. 2, a double-harvest variety), each having 10 tillers and three leaves, 10–15 cm tall, were transplanted into 16 black plastic containers (about 15 L) in a greenhouse on 31 April, 2013. Each cluster was supported in the centre of a grey foam lid, and the roots were immersed in a continuously aerated nutrient solution made of 4.4 mM NH_4NO_3, 0.64 mM NaH_2PO_4, 2 mM K_2SO_4, 4 mM $CaCl_2$, 1.5 mM $MgSO_4$, 1.4 mM KNO_3, 50 μM Fe(II)-ethylenediaminetetraacetic acid (EDTA), 10 μM H_3BO_4, 1.0 μM $ZnSO_4$, 1.0 μM $CuSO_4$, 5.0 μM $MnSO_4$, 0.5 μM Na_2MoO_4, and 0.2 μM $CoSO_4 \cdot 7H_2O$. To improve growth, we added SiO_2 (50–100 mg L^{-1}) and adjusted the pH to 5.6–5.8. After cultivation for 14 d, plants were transferred to solutions with different concentrations of P in form of monosodium orthophosphate: 0, 0.16, 0.64, and 2.56 mM. To grow plants under different P concentrations, $H_2PO_4^-$ was replaced by Cl^- at an equivalent Na^+ concentration. The nutrient solutions were changed every 5 d. The conditions in the greenhouse were as follows: 12-h photoperiod, day/night temperature of 29/20°C, the average PPFD of 600 μmol m^{-2} s^{-1}, and relative humidity of 80%.

Leaf length and width of the third fully expanded leaf from the top, tiller number, leaf number, and plant height were measured four weeks after the treatment. Fresh mass (FM) of leaf, sheath, culm, root, and total plant were also measured.

P content was determined with the vanado-molybdate method (Campbell and Sage 2006). Tissues stored at −18°C were brought to room temperature, and a subsample (approximately 0.25 g) was weighed and digested in a concentrated HNO_3:$HClO_4$ (3:1) at 175°C. Total phosphorus (P_{tot}) concentration was determined using a *UV-2410PC* spectrophotometer (*Shimadzu*, Tokyo, Japan). P_{tot} was fractionated into inorganic phosphorus (P_i) and organic phosphorus (P_o) (soluble ester phosphates and insoluble P_o). The required tissue mass was calculated from the P_{tot} concentration to give a subsample with a P_{tot} concentration lesser than the maximum P_i that could be precipitated, according to the method of Sugino and Miyoshi (1964). After weighing, the samples were kept at 4°C during the fractionation steps. Each sample was extracted four times in fresh 5% (v/v) perchloric acid for 30 min on a shaker and then centrifuged at 12,000 × *g* for 20 min. The supernatant (containing P_i and ester phosphates) was collected, and the tissue pellet was resuspended in 5% perchloric acid. For each wash, the P_i fraction in the supernatant was specifically precipitated using triethylamine and ammonium molybdate. The suspension was then centrifuged at 12,000 × *g* for 20 min. The pellet containing the P_i fraction was resuspended in 0.5 mL of water. The recovery rate from the supernatant after the specific precipitation of P_i with triethylamine and ammonium molybdate was 98 and 94%, respectively. The P_i fraction in the combined supernatants from each tissue sample was determined after acid digestion as described above for P_{tot}. P_o fraction was obtained by subtracting P_i fraction from P_{tot}.

Gas-exchange measurements were carried out with a *LI-6400* portable photosynthesis system (*Li-Cor*, Lincoln, NE, USA) (Yan *et al*. 2013a). The third fully expanded leaf from the top of a plant was measured. The leaf chamber was equilibrated at 24–26°C for at least 15 min in order to reach a steady state before the measurements. P_N, g_s, C_i, and transpiration rate (E) were determined at ambient CO_2 concentration of 350 μL L^{-1} and a temperature of 25.0 ± 0.5°C with a relative humidity of 80 ± 5% and a photon flux density of 1,200 μmol m^{-2} s^{-1}. All measurements were carried out from 9:00 to 11:00 h or from 14:30 to 16:30 h on sunny days. Each measurement was repeated six times, and the measurement site was located in the middle of a fully expanded blade. Estimation of the V_{cmax} and J_{max} were made by fitting a maximum likelihood regression below and above the inflexion of the P_N/C_i response using the method of McMurtrie and Wang (1993).

Chl was extracted by grinding 0.5 g of leaf tissue in 1 mL of 100% acetone with a pinch of calcium carbonate in a mortar. The extract was poured into a test tube and the mortar was rinsed with 100% acetone. The supernatant was then poured into the test tube to bring the final extract to 5 mL. The extract was filtered through a 0.45 μm syringe filter to remove debris. The absorbance of the filtered extract was determined with a *UV-2410PC* spectrophotometer (*Shimadzu*, Tokyo, Japan). Chl *a* and Chl *b* content was measured at absorbance wavelengths of 663 (A_{663}) and 645 nm (A_{645}), respectively, and concentrations were calculated using the equations given by Lichtenthaler (1987). Chl content was the sum of the Chl *a* and Chl *b* contents.

Chl *a* fluorescence parameters of the third fully expanded leaves were measured with a fluorescence imaging system (*M-Series Imaging-PAM*, *Walz*, Effeltrich, Germany) following the procedure described by Yan *et al.* (2013b). The F_v/F_m ratio is a measure of the maximal photochemical efficiency of PSII (Krause and Weis 1991). After the cessation of the actinic light, Φ_{PSII}, NPQ, q_P, and ETR were determined using saturating pulses added periodically for 5 min. Φ_{PSII}, NPQ, q_P, and ETR were exported by the software *Imaging-WIN* (*Walz*). q_P and NPQ were calculated according to Van Kooten and Snel (1990) using the following equations: $q_P = (F_m' - F_s)/(F_m' - F_0')$ and $NPQ = 1 - (F_m' - F_0')/(F_m - F_0)$. The actual Φ_{PSII} was calculated as defined by Genty *et al.* (1989) using the equation: $\Phi_{PSII} = (F_m' - F_s)/F_m'$, and ETR was calculated using the equation: $ETR = (F_m' - F_s)/F_m' \times PAR \times 0.5 \times 0.84$.

Statistical analysis was performed with *SPSS 8.0* software (*SPSS Inc.*, Chicago, IL, USA). Data were analysed using one-way analysis of variance (*ANOVA*) with P treatment as the main fixed factor in the model. Differences between the treatments were tested according to the *Tukey-Kramer*'s multiple test ($P = 0.05$). To ensure normality and homogeneity of variances, data were log-transformed when necessary.

Increasing the P concentration in the nutrient solution from 0 to 0.64 mM tended to stimulate plant growth, *e.g.*, plant height, leaf length, and tiller number increased by 30.7, 40.6, and 31.2%, respectively, and FM of leaf, sheath, culm, and total plant increased by 40.4, 39.0, 45.2, and 48.7%, respectively (Table 1). By contrast, increasing the P concentration to 2.56 mM showed suppressive effect on growth of Z. *latifolia*. The P concentration affected also considerably the root growth (Table 1). This is consistent with the observations of other researchers (Schachtman *et al*. 1998, De Groot *et al*. 2001, Chiera *et al*. 2002, Fujita *et al*. 2003, Kavanová *et al*. 2006, Moor *et al*. 2009, Naeem *et al*. 2010). The increase of the plant growth may be attributed to the promoted cell division (Radin and Eidenbock 1984, Fredeen *et al*. 1989, Rao and Terry 1989, Rodríguez *et al*. 1998, Clarkson *et al*. 2000, Chiera *et al*. 2002, Kavanová *et al*. 2006).

Root FM and root:shoot ratio were promoted by P, with the highest values being observed at the lower concentration of P (0.16 mM) (Table 1). The increased root:shoot ratio may be due to the enhanced root growth

Table 1. Plant growth parameters of *Zizania latifolia* four weeks after phosphorus treatment. The plants were subjected to different phosphorus concentrations. Values (means ± SE, $n = 6$) followed by *different letters* between different phosphorus concentrations are significantly different according to the *Tukey-Kramer* multiple test ($P<0.05$). FM – fresh mass.

Parameters	Phosphorus concentration [mM]			
	0	0.16	0.64	2.56
Plant height [cm]	72.70 ± 2.63^{c}	80.30 ± 4.11^{b}	95.00 ± 4.75^{a}	90.70 ± 5.53^{ab}
Leaf length [cm]	50.30 ± 2.52^{c}	59.70 ± 2.98^{b}	70.70 ± 3.53^{a}	64.30 ± 4.22^{ab}
Leaf width [cm]	2.27 ± 0.11^{b}	2.37 ± 0.12^{ab}	2.53 ± 0.13^{a}	2.47 ± 0.14^{a}
Leaf number	3.33 ± 0.17^{bc}	3.67 ± 0.18^{b}	4.66 ± 0.25^{a}	4.66 ± 0.23^{a}
Tiller number	20.20 ± 0.75^{c}	22.30 ± 0.52^{b}	26.50 ± 0.55^{a}	25.20 ± 0.75^{ab}
Root length [cm]	32.10 ± 2.12^{c}	50.80 ± 3.43^{a}	50.30 ± 3.65^{a}	41.50 ± 2.83^{b}
Leaf FM [g]	3.12 ± 0.13^{c}	3.41 ± 0.14^{b}	4.38 ± 0.22^{a}	4.15 ± 0.25^{ab}
Sheath FM [g]	11.61 ± 0.58^{c}	12.83 ± 0.60^{b}	16.14 ± 0.81^{a}	15.33 ± 0.92^{ab}
Culm FM [g]	7.92 ± 0.25^{c}	9.56 ± 0.48^{b}	11.50 ± 0.58^{a}	10.60 ± 0.73^{ab}
Root FM [g]	5.38 ± 0.27^{d}	10.56 ± 0.43^{a}	9.66 ± 0.45^{b}	7.38 ± 0.37^{c}
Total plant FM [g]	28.03 ± 1.23^{c}	36.36 ± 1.65^{b}	41.68 ± 2.06^{a}	37.46 ± 2.27^{ab}
Root:shoot ratio	0.23 ± 0.01^{c}	0.41 ± 0.01^{a}	0.30 ± 0.01^{b}	0.24 ± 0.01^{c}

and reduced shoot growth (Table 1) (Mollier and Pellerin 1999). The increase in the root growth is probably an adaptive response of plant to low P (Vance *et al*. 2003), because increased production of root-hair facilitates acquiring P more efficiently (Lambers *et al*. 2006, Hammond and White 2008).

There was an increase in content of P_{tot} and P_i with elevation in P concentration, however, the highest P_o content was observed at the P of 0.64 mM (Table 2), indicating that at low P, leaf P content depends mainly on the transport from the roots and the mobilization of stored phosphate from older leaves (Schachtman *et al*. 1998). In addition, reduced hydraulic conductance resulting from P deficiency may affect the distribution of phosphate and nitrate ions between shoots and roots (Radin and Mathews 1989). The decreased number of tillers seemed to be linked to low P concentration in plant (Table 1) (Rodríguez *et al*. 1999).

Gas exchange in *Z. latifolia* plants was significantly promoted by P application, *e.g.*, P_N, g_s, and E increased by 52.3, 76.2, and 39.9%, respectively, at 0.64 mM(P) compared to 0 mM(P). However, C_i was significantly inhibited by P application (Table 2). In the present study, limiting photosynthesis at low concentration of P is possibly associated with the decreased g_s and E (Pieters *et al*. 2001), and low sink demand for assimilates that may result in the reduction in source activity or photoassimilate partitioning (Radin 1984, Rao and Terry 1989, Jacob and Lawlor 1991). The declined P_N is accompanied by decreased g_s and increased C_i, suggesting nonstomatal factors involved in this process (Fredeen *et al*. 1990, Jacob and Lawlor 1991).

Additionally, V_{cmax} and J_{max} were also significantly lowered at low P (0.16 mM) (Table 2). Reductions in V_{cmax} may result from reductions in Rubisco activation state or in Rubisco content (Sharkey 1985). It is reported that reduced photosynthetic capacity due to P limitation frequently occurs; that may be due to decreased both Rubisco activity and the RuBP regeneration capacity (Lewis *et al*. 1994, Campbell and Sage 2006). In this study, our results showed that low-P (0.16 mM) caused a low J_{max}, indicating RuBP regeneration was reduced (Jacob and Lawlor 1992).

Chl *a* fluorescence was significantly affected by P application (Table 2). The reduction in the F_v/F_m under the lower P concentration could be interpreted as a result of a decrease in Chl synthesis. The reduction in q_P and increase of NPQ indicated that low P (0.16 mM) increased excitation pressure on PSII and contributed to the closure of PSII reaction centres, which induced a lower possibility of electron transport from PSII to PSI. Accordingly, Φ_{PSII}, closely related to the quantum yield of noncyclic electron transport, decreased in plants, resulting in a significant reduction of photosynthetic efficiency of PSII (Plesničar *et al*. 1994, Müller *et al*. 2001, Li *et al*. 2004). High P (2.56 mM) caused slight decrease in plant height, leaf length, tiller number, and plant biomass (Table 1). This corroborated the report that high P decreased the biomass (Wu *et al*. 2009). Hindrance of plant growth by high P could be at least in part attributed to the inhibited transport

Table 2. Effects of phosphorus concentration on the phosphorus content, chlorophyll content, photosynthesis, and chlorophyll fluorescence parameters in leaves of *Zizania latifolia*. The plants were subjected to different phosphorus concentrations for four weeks. Values (means ± SE, n = 6) followed by *different letters* between different phosphorus concentrations are significantly different according to the *Tukey-Kramer* multiple test (P<0.05). Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; ETR – electron transport rate; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; J_{max} – maximum rates of RuBP regeneration; NPQ – nonphotochemical quenching; P_i – inorganic phosphorus; P_N – net photosynthetic rate; P_o – organic phosphorus; P_{tot} – total phosphorus; Φ_{PSII} – effective quantum yield of PSII photochemistry; q_P – photochemical quenching coefficient; V_{cmax} – maximum carboxylation rate of Rubisco.

Parameters	Phosphorus concentration [mM]			
	0	0.16	0.64	2.56
P_{tot} [mg g^{-1}(DM)]	4.88 ± 0.14^{d}	5.38 ± 0.22^{c}	6.22 ± 0.30^{b}	6.88 ± 0.24^{a}
P_i [mg g^{-1}(DM)]	2.30 ± 0.07^{d}	2.61 ± 0.11^{c}	3.12 ± 0.16^{b}	3.96 ± 0.15^{a}
P_o [mg g^{-1}(DM)]	2.58 ± 0.07^{c}	2.77 ± 0.11^{b}	3.10 ± 0.14^{a}	2.92 ± 0.09^{ab}
Chl [mg g^{-1}(FM)]	1.61 ± 0.09^{bc}	1.74 ± 0.11^{b}	2.05 ± 0.13^{a}	1.94 ± 0.12^{ab}
P_N [μmol(CO_2) m^{-2} s^{-1}]	7.29 ± 0.14^{c}	8.67 ± 0.36^{b}	11.10 ± 0.70^{a}	9.60 ± 0.93^{ab}
g_s [mol(H_2O) m^{-2} s^{-1}]	0.21 ± 0.02^{c}	0.27 ± 0.03^{b}	0.37 ± 0.03^{a}	0.31 ± 0.04^{ab}
C_i [μmol(CO_2) mol^{-1}]	335.00 ± 13.00^{a}	323.00 ± 11.00^{a}	298.00 ± 7.00^{bc}	311.00 ± 7.00^{b}
E [mmol(H_2O) m^{-2} s^{-1}]	3.56 ± 0.22^{c}	4.12 ± 0.25^{b}	4.98 ± 0.46^{a}	4.51 ± 0.32^{ab}
V_{cmax} [μmol(CO_2) m^{-2} s^{-1}]	49.60 ± 3.32^{c}	59.80 ± 4.58^{b}	71.60 ± 5.87^{a}	63.20 ± 6.19^{ab}
J_{max} [μmol(CO_2) m^{-2} s^{-1}]	115.60 ± 7.61^{c}	137.50 ± 10.5^{b}	162.80 ± 13.40^{a}	145.40 ± 14.7^{ab}
F_v/F_m	0.74 ± 0.01^{b}	0.76 ± 0.01^{ab}	0.78 ± 0.01^{a}	0.77 ± 0.01^{a}
Φ_{PSII}	0.32 ± 0.01^{c}	0.35 ± 0.01^{b}	0.40 ± 0.01^{a}	0.37 ± 0.02^{ab}
NPQ	0.37 ± 0.01^{a}	0.35 ± 0.01^{ab}	0.31 ± 0.00^{c}	0.33 ± 0.01^{b}
q_p	0.50 ± 0.01^{c}	0.55 ± 0.02^{b}	0.63 ± 0.02^{a}	0.59 ± 0.02^{ab}
ETR [μmol m^{-2} s^{-1}]	24.60 ± 0.84^{c}	27.90 ± 0.69^{b}	33.25 ± 2.20^{a}	30.58 ± 1.39^{ab}

of P from the roots to the shoots, as indicated by the reduced root:shoot P concentration ratio. Our results showed that high P (2.56 mM) decreased P_N, which may be associated with P accumulation (Table 2) (Shane *et al*. 2004) and the reduced ETR (Duchein *et al*. 1993). This is consistent with the report that high P decreased light-saturated P_N in sunflower plants (Plesničar *et al*. 1994). Our results showed that high P (2.56 mM) caused the increase in NPQ but the decrease in q_P, which corroborated the results of previous studies (Plesničar *et al*. 1994, Li *et al*. 2004).

In conclusion, the growth and photosynthetic processes of *Z. latifolia* plants were greatly affected by P concentration. The reduced growth would be attributed to the lowered photosynthetic ability under P deficient (0 mM) or low P (0.16 mM) conditions as observed through fluorescence parameters, such as reduced Φ_{PSII}, q_P, and ETR.

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