

## Effects of soil moisture on *Phragmites australis* (Cav.) allelochemicals in soil and on growth of *Phalaris arundinacea* L. in Chinese Wetland

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(Received in Revised Form: July 8, 2020)

### ABSTRACT

We studied the effects of soil moisture on *Phragmites australis* [(Cav.) Trin. ex Steudel]. allelochemicals in soil and on growth of *Phalaris arundinacea* L. in Chinese Wetland. Results showed that the relative water content (RWC) of soil in co-existing *P. australis* (Cav.)-*P. arundinacea* L. community decreased with increasing elevation of beach wetland and this increased the total phenolics content (TPA) in rhizosphere soil. The increased TPA in soil increased the magnitude of allelopathic inhibition of *P. australis* (Cav.) on the growth and physiological parameters of *P. arundinacea* L. The effects of soil moisture on *P. australis* (Cav.) allelopathic effects on the *P. arundinacea* L. were evident on the equations.

**Key words:** Allelochemicals, allelopathic inhibition, allelopathy, fitting equation, growth, phenolic acids, *Phragmites australis*, *Phalaris arundinacea*, rhizosphere soil, soil moisture

### INTRODUCTION

Allelopathy is natural ecological phenomenon, in which the living organisms produce and release the allelochemicals in the environment that affects the growth, development, reproduction and survival of other living organisms in the surrounding environment (3). Allelopathy effectively influences the succession rate of plant communities, the sequence of species occurrence and composition of stable communities (13,23). *Phragmites australis* (Cav.) is allelopathic plant, which is inhibitory to other plants (2,20,21). In the Eastern United States, *P. australis* (Cav.) is most invasive plant in marsh and wetland communities due to its strong allelopathic potential (16). In China, *P. australis* (Cav.) allelopathically inhibits the invasive plants [*Solidago canadensis* L. and *Spartina alterniflora* Loisel. (11,24)]. The *P. australis* (Cav.) inhibits the growth of other plants mainly by releasing the water soluble phenolic allelochemicals in water (9,13).

Based on these observations, Fu *et al.* (9) studied the succession of plant communities in the Zhenjiang Waterfront Wetlands along the mid-lower reaches of the Yangtze River in China. He found that *P. australis* (Cav.) replaced the pioneer species of *Phalaris arundinacea* L. through allelopathy during the community succession. However,

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the replacement occurred gradually with increasing elevation of wetland beach (6,9,25). The allelopathic inhibition of *P. australis* (Cav.) on the *P. arundinacea* L. gradually increased with elevation of wetland beach. We hypothesized that the gradual increase in the intensity of allelopathic inhibition of *P. australis* (Cav.) on *P. arundinacea* L. with elevation of wetland beach was also due to the decrease in soil moisture (19,22). To verify this hypothesis, (i). we studied the effects of soil moisture content on *P. australis* (Cav.) allelopathy on the *P. arundinacea* L., (ii). we determined the total phenolic acid (TPA) content in rhizosphere soil of *P. australis* (Cav.) in coexisting community under different soil moisture regimes and (iii). the allelopathic effects of TPA Contents in soil of *P. australis* (Cav.) on the growth and development of *P. arundinacea* L. This study may help in identifying the ecological processes (competition, coexistence and population displacement) in plants community succession.

## MATERIALS AND METHODS

### I. Experimental site

All field experiments were done in Zhenjiang Waterfront Wetlands along the mid-lower reaches of the Yangtze River, China (32°15'N and 119°28'E). Annual mean temperature is 15.4 °C and Annual precipitation is 1074 mm. The primary succession in the plant community in this wetland occurs with the gradual elevation of the wetland beach. The vegetation succession in this wetland passes through 3- community types: (i). Initial community of *P. arundinacea* L., (ii). Intermediate transitional community of *P. arundinacea* L.+ *P. australis* (Cav.) and (iii). Climax community of *P. australis* (Fig. 1) (4). The dominant perennial species of *P. arundinacea* L. and *P. australis* in the community are from Gramineae family. The Photographs showed that *P. arundinacea* is low growing (1.6 m height) and *P. australis* is tall growing (3.7 m). The *P. australis* allelopathic effects on *P. arundinacea* L. causes the community succession (9).



Figure 1. The three community types over the plant community succession in study area wetland

### I. Experimental details

In this study, we determined the allelopathic effect of *P. australis* (Cav.) on *P. arundinacea* L. with the decrease in soil moisture. In May 2017, we selected the slightly sloping area (slope:  $h/l \approx 0.03$ ) of the vigorously growing *P. arundinacea* L.+*P. australis* (Cav.) community, with similar density of *P. australis* (Cav.) in Zhenjiang Waterfront Wetland. Five consecutive plots of 30 m<sup>2</sup> (5 m × 6 m) area were made 2.0 m apart following the elevation of the wetland beach. Then 3-Quadrants (1 m × 1 m) were marked randomly in each plot (Fig. 2).

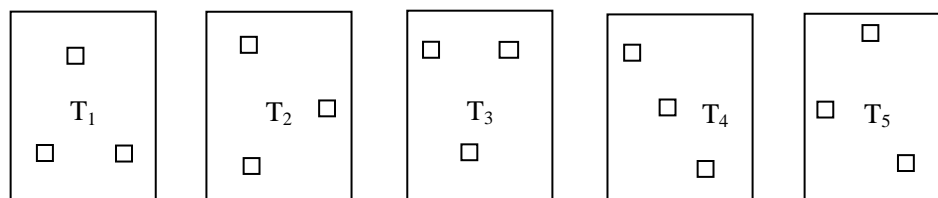


Figure 2. Diagrammatic positions of quadrants in the plots

Note: The rectangle represents the plot and the square represents the quadrants.

The experimental treatments were 5-soil moisture levels viz., T<sub>1</sub> (97.5-99.5 %), T<sub>2</sub> (90.5-92.5 %), T<sub>3</sub> (84.5-86.5 %), T<sub>4</sub> (76.5-78.5 %), T<sub>5</sub> (71.5-73.5 %). The T<sub>1</sub> (Control) had 100 % soil relative water content (RWC). Treatments were replicated thrice in Randomized. Experimental Design. The various soil moisture contents in different treatments were maintained by regular manual watering.

### III. Parameters studied in *P. arundinacea* L.

(i). **Photosynthetic Parameters:** We measured the Net photosynthetic rate, Stomatal conductance and Intercellular CO<sub>2</sub> concentration using an LI-6400 System (LI-COR 6400, USA), from 09:00 to 09:30 on sunny day May 14, 2018 from the top 3- fully expanded leaves of *P. arundinacea* L. plants. Light intensity was set as 1100 μmol m<sup>-2</sup> s<sup>-1</sup> and was measured using the light-emitting diode (LED) light source built in LI-COR 6400 (8).

(ii). **Enzymes:** Nine uniform and vigorous *P. arundinacea* L. plants were selected from each treatment. Top four leaves of each plant were collected and stored in liquid nitrogen to measure antioxidative enzyme activities in laboratory. Enzyme were extracted at 0 to 4 °C. Samples from fresh mature leaves (0.5 g) were homogenized in ice cold mortar in 5 ml of 50 mM sodium phosphate buffer (pH 7 for CAT and pH 7.8 for SOD and POD) containing 1 mM EDTA-Na<sub>2</sub>. The supernatant was used to find the SOD, CAT and POD activities after centrifugation (1,000g, 20 min) (7) as under.

(A) **SOD Activity:** It was assayed by the nitroblue tetrazolium (NBT) method (10). After fully mixing the supernatant with the reaction solution, the colour was developed under 4000 LX fluorescent lamp for 20 minutes, the absorbance at 560 nm was measured.

(B) **CAT Activity:** It was measured spectrophotometrically. The supernatant and the reaction solution were mixed thoroughly and 300 μl of H<sub>2</sub>O<sub>2</sub> was continuously added to record the absorbance within 4 min at 240 nm.

**(C) POD Activity:** It was measured using the method of Maehly and Chance (12). After the supernatant and the reaction solution were mixed, the solution was incubated in water bath at 34°C for 3 min and the absorbance in 4 min was recorded at 470 nm.

**(D) MDA content:** It was measured as per the method of Esterbauer and Cheeseman (1,5). Add 2 mL of 0.67 % Thibarbituric acid to the supernatant, mix and boil for 30 min in boiling water bath, centrifuge for 10 min at 3 000 r/min, after cooling measure absorbance colorimetrically at 450, 532 and 600 nm with ultraviolet-visible spectrophotometer.

**(iii). Plant growth:** Plant height was measured from 10-plants of *P. arundinacea* per treatment by measuring the length of the main stem from the bottom to the top. These plants were harvested to record their main stem biomass (dry weight: dried at 80 °C for 12 h to constant weight).

**(IV). *P. australis* (Cav.) Soil Parameters:**

*P. australis* (Cav.) releases many allelochemicals (including the phenolic acids) in the rhizosphere soil. From each treatment, we collected 3-soil samples up to 30 cm depth from each quadrant. Since there were 3- Quadrants in each plot, hence, 9- soil samples were collected from each treatment. These were mixed to make one composite soil sample. These 5- Composite soil samples were immediately transported to the laboratory. One part of each Composite soil sample was used to measure the soil RWC, gravimetrically: The RWC of soil sample was used to calculate the difference between the fresh weight and dry weight (dried at 105 °C for 12 h to constant weight) (1). The other part of soil sample was used to measure the TPA (Total Phenolic acids) of rhizosphere soil. TPA content of the extracts was determined according to the Folin-Ciocalteu spectrophotometric method with slight modifications. Briefly, 0.5 mL soil sample extract solution was mixed with 2.5 ml of 10-times diluted Folin-Ciocalteu's phenol reagent and allowed to react for 5 min. Then 2 mL of 75 g/L sodium carbonate (Na<sub>2</sub>CO<sub>3</sub>) solution was added. The final volume was made up to 10 mL with deionized water. After reaction for 1 h at room temperature, the absorbance was measured at 760 nm (15).

**IV. Statistical analysis**

All Data obtained from different treatments were analyzed using SPSS software package. One-way ANOVA was performed. The least significant difference multiple comparison test was conducted at  $\alpha=0.05$ .

## RESULTS AND DISCUSSION

**Relative water content and Total Phenolic Acid (TPA) in soil**

(i). **RWC:** The soil RWC of each treatment was analysed. Soil RWC gradually decreased with increasing elevation of wetland beach. In treatments T<sub>1</sub>, T<sub>2</sub>, T<sub>3</sub>, T<sub>4</sub> and T<sub>5</sub>, the mean RWC of soil was 98.44 %, 91.54 %, 85.68 %, 77.84 % and 72.57 %, respectively. Compared with soil RWC of T<sub>1</sub>, the RWC of T<sub>2</sub>, T<sub>3</sub>, T<sub>4</sub> and T<sub>5</sub> treatments were decreased by 7.01 %, 12.96 %, 20.92 % and 26.28 %, respectively. Thus increase

in elevation of wetland beach caused variations in the RWC of all treatments.

(ii). **TPA:** In contrast with soil RWC, the TPA content in rhizosphere soil gradually increased with increasing elevation of wetland beach (Figure 3). TPA in rhizosphere soil of T<sub>1</sub> was 32.88 ug g<sup>-1</sup>. The TPA of T<sub>2</sub>, T<sub>3</sub>, T<sub>4</sub> and T<sub>5</sub> was 3.80 %, 26.52 %, 53.13 % and 75.18 % higher, respectively, than control (T<sub>1</sub>). The variations in the TPA of rhizosphere soil from different treatments were significant and was correlated with the increasing elevation of wetland beach. The lower solubility of phenolic acids in water increased the TPA in rhizosphere soil, with increasing elevation of wetland beach. These results showed that the TPA in rhizosphere soil increased with the decrease of soil RWC.

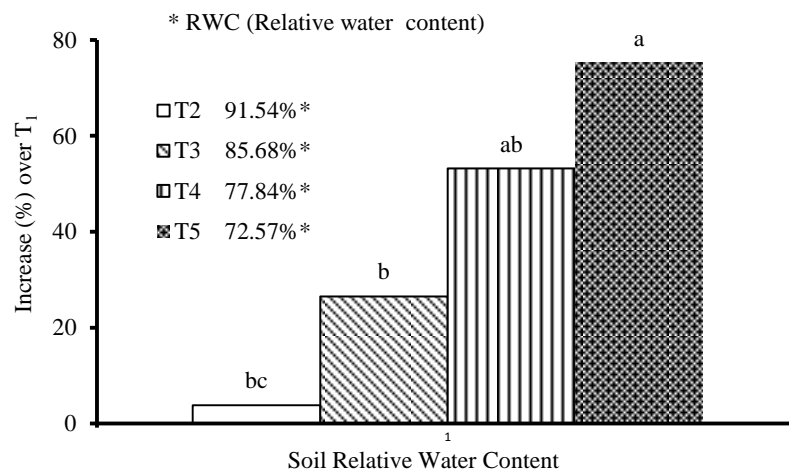


Figure 3. Effects of soil water content on TPA (Total Phenolic acids) in rhizosphere soil of *P. australis*

#### Growth and photosynthetic, physiological parameters

(i). **Plant growth:** In fact, *P. arundinacea* grows well in wetland environment, but is also very tolerant to drought (12). When the soil RWC reaches a certain value, differences in soil RWC affects the growth and development of *P. arundinacea* (13). Field investigations at the experimental site showed that the growth of different *P. arundinacea* populations was similar in all the soil moisture ranges. Therefore, we presumed that differences in growth and physiology among the various treatments in this study did not directly attribute to the differences in soil RWC, but attributed to variations in TPA contents, caused by the different levels of soil RWC.

(ii). **Photosynthetic parameters:** The growth and physiological, photosynthetic parameters of *P. arundinacea* in each treatment are given in Figure 4 and Figure 5. Both the growth parameters (plant height and main stem biomass) and the photosynthetic parameters of Net photosynthetic rate and Stomatal conductance of *P. arundinacea* gradually decreased with increasing elevation of wetland beach. In T<sub>2</sub>, T<sub>3</sub>, T<sub>4</sub> and T<sub>5</sub>

treatments, the decrease in plant height was 3.69 %, 8.47 %, 13.98 % and 24.78 % and the decrease in main stem biomass was 2.23 %, 11.04 %, 17.63 % and 19.45 %, respectively, than in control ( $T_1$ ).

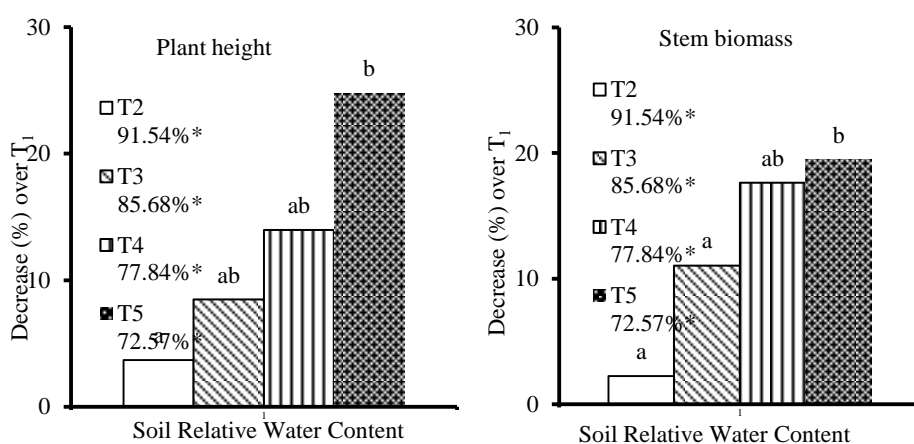


Figure 4. Effects of soil water content on growth (Plant height and Stem biomass) of *P. arundinacea*

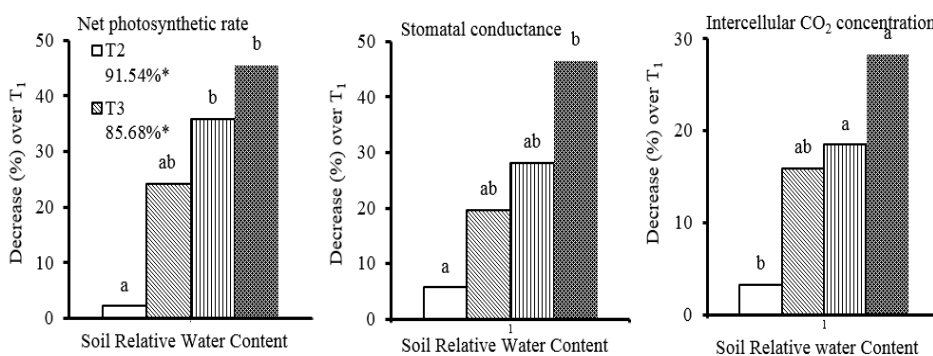


Figure 5. Effects of soil water content on photosynthetic parameters (Net photosynthetic rate, Stomatal conductance and Intercellular  $CO_2$  concentration) of *P. arundinacea*

The photosynthetic physiological parameters (Net photosynthetic rate, Stomatal conductance and Intercellular  $CO_2$  concentration) in  $T_2$ ,  $T_3$ ,  $T_4$  and  $T_5$  treatments decreased than in  $T_1$ , from  $T_2$  to  $T_5$ . The decrease in Net photosynthetic rate was 2.14 %, 24.12 %, 35.80 % and 45.56 % and the decrease in Stomatal conductance was 5.71 %, 19.59 %, 28.16 % and 46.53 %, respectively, compared to control ( $T_1$ ). On the contrary, the photosynthetic parameter of Intercellular  $CO_2$  concentration gradually increased with increasing elevation of wetland beach. Intercellular  $CO_2$  concentrations in treatments  $T_2$ ,  $T_3$ ,  $T_4$  and  $T_5$  were 3.28 %, 15.88 %, 18.47 % and 28.32 % higher than Control  $T_1$ ,

respectively. In treatments T<sub>1</sub> to T<sub>5</sub>, there were significant differences ( $p < 0.05$ ) in all above parameters. These results indicated that the growth and photosynthesis of *P. arundinacea* were gradually inhibited with increasing elevation of wetland beach.

(iii). **Enzymes:** The environmental stress causes the production and accumulation of reactive oxygen species (ROS). The antioxidant enzymes (SOD, CAT and POD) of *P. arundinacea*, functions as one of defence mechanisms to prevent the damage from ROS. However, the MDA indicates the degree of oxidative damage. The SOD, CAT, POD and MDA shows whether, the plants are under environmental stress and the extent of stress (5). The antioxidative enzyme activities of *P. arundinacea* varied in treatments (Figure 6). The SOD, CAT and POD of *P. arundinacea* initially increased and then gradually decreased with increasing elevation of wetland beach. However, peaks of CAT with  $33.3 \text{ U g}^{-1} \text{ min}^{-1}$  and POD with  $308.3 \text{ U g}^{-1} \text{ min}^{-1}$  were recorded in T<sub>3</sub>, whilst, the peak of SOD ( $341.5 \text{ U g}^{-1} \text{ min}^{-1}$ ) was in T<sub>4</sub>. This showed that the sensitivities of different antioxidant enzymes depended on soil moisture. The MDA content of *P. arundinacea* increased continuously with increasing elevation of wetland beach. The MDA contents of T<sub>2</sub>, T<sub>3</sub>, T<sub>4</sub> and T<sub>5</sub> were 5.33 %, 40.63 %, 63.83 % and 85.30 %, higher than T<sub>1</sub>, respectively. In treatments T<sub>1</sub> to T<sub>5</sub> the differences in all above parameters were significant at  $p < 0.05$ . These results indicated that the degree of allelopathic inhibition on *P. arundinacea* increased gradually with increasing elevation of wetland beach.

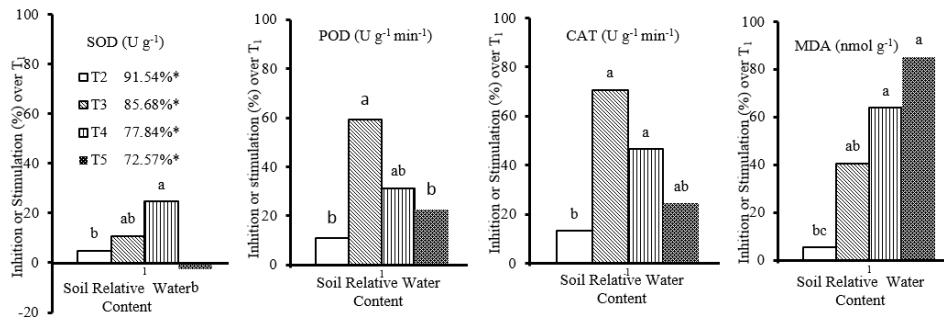


Figure 6. Effects of soil water content on activities of enzymes of SOD, POD, CAT and MDA of *P. arundinacea*. Note: SOD, POD, CAT and MDA stand for Superoxide Dismutase, Catalase, Peroxidase, and Malondialdehyde, respectively.

*P. arundinacea* thrives both in wetland environment and in drought (17). Field investigations at the experimental site showed that the growth of different *P. arundinacea* populations was similar in all the soil moisture ranges. Therefore, variations in the growth and physiology of *P. arundinacea* among the different treatments did not directly depend on the soil RWC, but on the TPA contents in rhizosphere soil, which was influenced by soil RWC.

#### Correlations of different parameters

We studied the effects of soil moisture on the *P. australis* allelopathy, which influenced the growth of *P. arundinacea* plants. We determined the correlations analyses among the soil RWC, TPA, growth and physiological parameters of *P. arundinacea* (Table

1). The environmental factors of soil RWC and TPA in rhizosphere soil were significantly corrected with growth and physiological parameters of *P. arundinacea*. No significant correlation was observed between the enzymes (SOD, CAT and POD) and environmental factors (soil RWC and TPA), because the enzymes initially increased and then decreased with reduction in soil moisture. Therefore, except the enzymes (SOD, CAT and POD), all other growth and physiological parameters of *P. arundinacea* were affected by the magnitude of allelopathic inhibitory effects of *P. australis* on *P. arundinacea*, with changes in soil moisture. Thus the selected parameters of Net photosynthetic rate, plant height and main stem biomass of *P. arundinacea* can be used to determine the effects of *P. australis* allelopathy on *P. arundinacea* in relation to the soil moisture.

Table 1. Correlation analyses between environmental factors and growth and physiological parameters

	RWC	TPA	Height	Biomass	SOD	POD	CAT	MDA	Pn	Cond
TPA	-0.9836**									
Height	0.9811**	-0.9961**								
Biomass	0.9706**	-0.9492*	0.9302*							
SOD	-0.2574	0.1617	-0.1025	-0.3705						
POD	-0.4638	0.3486	-0.3226	-0.6101	0.4825					
CAT	-0.4772	0.3595	-0.3243	-0.6305	0.6145	0.9872**				
MDA	-0.9869**	0.9979**	-0.9900**	-0.9675**	0.2086	0.4027	0.4164			
Pn	0.9901**	-0.9938**	0.9840**	0.9780**	-0.2471	-0.4403	-0.4568	-0.9988**		
Cond	0.9791**	-0.9895**	0.9931**	0.9446*	-0.0782	-0.4028	-0.3920	-0.9874**	0.9833**	
Ci	-0.9762**	0.9710**	-0.9683**	-0.9725**	0.1482	0.5334	0.5216	0.9782**	-0.9802**	-0.9886**

Note:  $R_{.05}=0.8780$ ;  $R_{.01}=0.9590$ ; \* and \*\* indicate significant and extremely significant correlations, respectively.

### Equations of allelopathy response to soil moisture

In this study, the 5-parameters (TPA, plant height, biomass, net photosynthesis and MAD) of *P. arundinacea* were selected to construct different fitting equations between each parameter and soil moisture level (Figure 7). By using the percent decrease in RWC compared with  $T_1$  as the independent variable (X) and the percent change (decrease or increase) in each selected parameter compared with  $T_1$  as the dependent variable ( $Y_i$ ). We obtained the fitting equations and curves of response of allelopathy to soil moisture (Figure 7). This Figure showed that the coefficient of determination of each fitting equation was  $> 0.9982$  with a unitary quadratic or cubic equation. These results indicated that excellent fitting effects were achieved between each selected parameter and soil moisture.

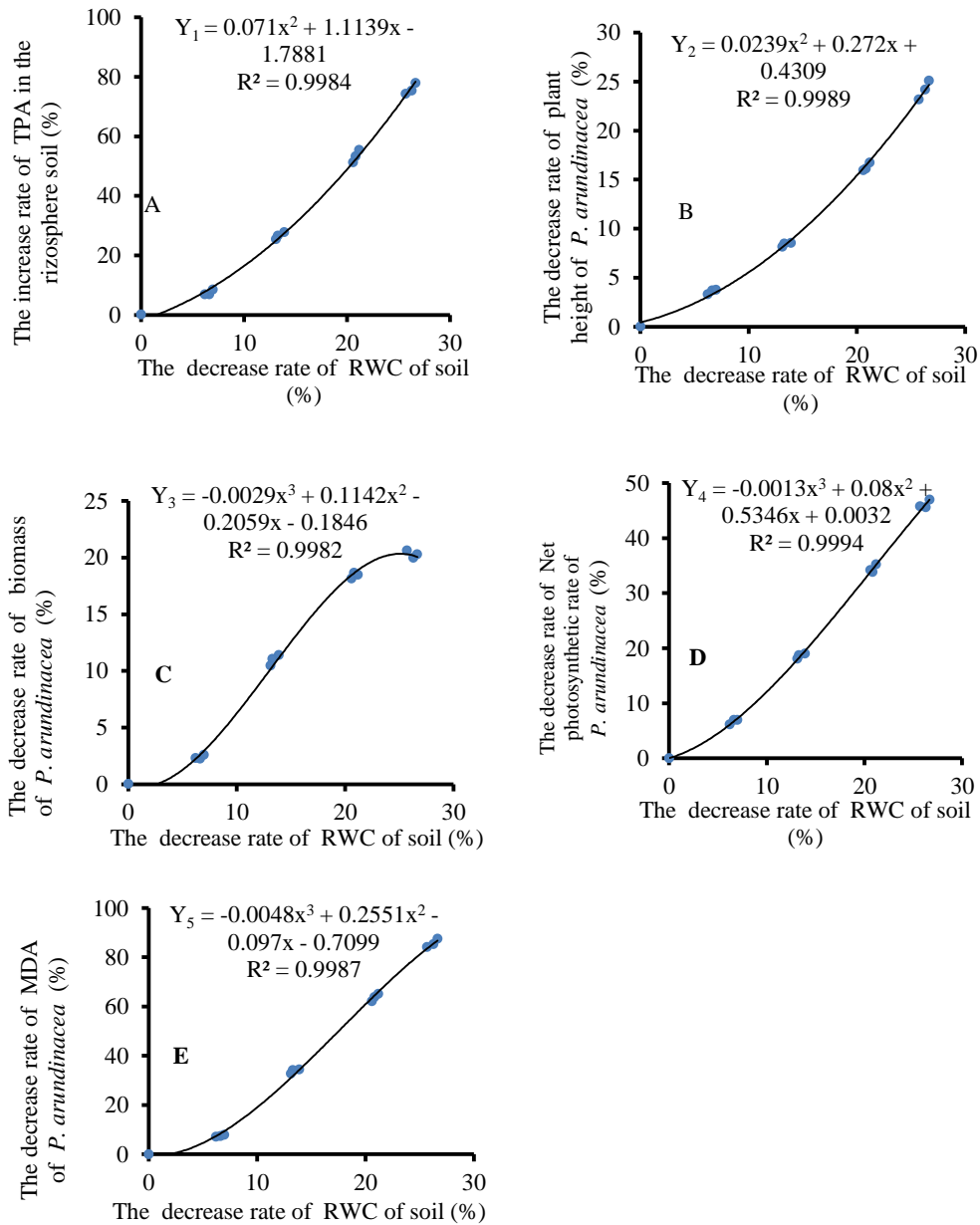


Figure 7. Fitting of allelopathy response of on *P. arundinacea* to soil moisture

Note: A:TPA, B: Plant height, C: Main stem biomass, D: Net photosynthetic rate, E: MDA to the soil moisture (RWC)

## CONCLUSIONS

The decrease of soil moisture in the coexisting *P. australis*-*P. arundinacea* community increased the amount of allelochemicals [i.e. total phenolic acids (TPA)] in rhizosphere soil. These allelochemicals ameliorated the inhibitory allelopathic effects of *P. australis* on the net photosynthesis and thereby on the growth (height, biomass) of *P. arundinacea*. The response of each parameter to soil moisture content can be fitted well, using a unitary quadratic or cubic equation. The decreased soil moisture directly increased the TPA Contents in rhizosphere soil of *P. australis* and thereby exerted the inhibitory allelopathic effects on the *P. arundinacea* and thus the hypothesis was verified.

## ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China [31370448], Major Projects of Natural Science Research in Colleges and Universities, Jiangsu Province [15KJA2100001], Postgraduate Research & Practice Innovation Program of Jiangsu Province [SJKY19\_2528], the Priority Academic Program Development of Jiangsu Higher Education Institutions [PAPD-2018-87] and High-tech Key Laboratory of Agricultural Equipment and Intelligentization of Jiangsu Province.

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