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Effects of exogenous phenolic acids on photosystem functions and photosynthetic electron transport rate in strawberry leaves

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Abstract

Our study investigated the physiological and biochemical basis for the effects of exogenous phenolic acids on the function of the photosynthetic apparatus and photosynthetic electron transport rate in strawberry seedlings. Potted seedlings of the strawberry (*Fragaria* × *ananassa* Duch.) were used. Syringic acid inhibited net photosynthetic rate and water-use efficiency decreased. Additionally, primary quinone electron acceptor of the PSII reaction centre, the PSII reaction centre and the oxygen evolving complex were also impaired. Both the maximum quantum yield of the PSII primary photochemistry and the performance index on absorption basis were depressed, resulting in reduced function of the photosynthetic electron transport chain. Otherwise, low phthalic acid concentrations enhanced photosynthetic capacity, while high concentrations showed opposite effects. Syringic acid exhibited a higher toxic effect than that of phthalic acid which was more evident at higher concentrations.

Additional key words: chlorophyll fluorescence; gas exchange; phenolic acid.

Introduction

The strawberry fruit is known for its sweet and juicy taste, rich nutrients, and abundant protein and vitamins (Tan *et al.* 2003). Strawberry is primarily grown as an annual crop. However, long-term continuous cropping at the same plots easily leads to weak growth of strawberry plants, yield reduction, and quality deterioration (the so-called soil sickness). The soil sickness phenomenon is particularly prominent under facility cultivation, which has become a major limiting factor in facility strawberry production (Cao and Wang 2007). Investigation of photosynthetic and physiological mechanism underlying long-term soil sickness is critical for high efficiency and high quality of strawberry facility cultivation.

Phenolic acids have been shown to be important factors that cause crop soil sickness (Schutter *et al.* 2001, Asao *et al.* 2008, Han *et al.* 2008). These compounds primarily originate from decomposition of plant residues and root exudation, among other sources. When they accumulate to a certain amount in the soil, phenolic acids exhibit an inhibitory effect on crop growth during the next cropping season (Inderjit *et al.* 2003, Hiradate *et al.* 2005, Asaduzzaman *et al.* 2012). Zhen (2003) identified six phenolic acids [phthalic acid (PA), p-hydroxybenzoic acid, syringic acid (SA), vanillic acid, ferulic acid, and benzoic acid] among decomposition products of strawberry roots from a plot under continuous strawberry cropping. The

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Abbreviations: ABS – reaction center area; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; ETR – electron transport rate; F_j – fluorescence yield at 2 ms; F_k – fluorescence yield at 300 µs; F_m – maximal fluorescence yield of the light-adapted state; FM – fresh mass; F_o – minimal fluorescence yield of the dark-adapted state; F_v/F_m – maximum quantum yield of PSII primary photochemistry; g_s – stomatal conductance; MR/MR_0 – modulated reflection of PSI at 820 nm; OEC – oxygen evolving complex; PA – phthalic acid; PI_{ABS} – performance index on absorption basis; P_N – net photosynthetic rate; P700 – the chlorophyll *a* maximum absorption peak of molecules at 700 nm; RC – the energy absorbed by active reaction center; SA – syringic acid; V_k – relative variable fluorescence at 300 µs; V_j – relative variable fluorescence at the J-step; V_{PSI} – MR/MR_0 maximal slope descending; $V_{PSI+PSII}$ – MR/MR_0 maximal slope increasing; W_k – relative variable fluorescence at the K-step; WUE – water-use efficiency (= P_N/E); Ψ_o – the ratio of trapped exciton electrons to other electron acceptors downstream of Q_A.

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verification test for phenolic acids showed that the root and shoot growth of tissue-cultured strawberry seedlings was inhibited to a certain degree. Huang *et al*. (2010) indicated that phenolic acids affected photosystem functions in cowpea (*Vigna sinensis*) leaves primarily through depressed root functions. When mulberry plants were treated with exogenous o-methoxybenzoic acid, chlorophyll (Chl) fluorescence parameters, such as the primary conversion of light energy by PSII (Φ_{PSII}) and electron transport rate (ETR) decreased. These changes resulted in lower ATP and NADPH production in the photosynthetic apparatus, which decreased the carbon assimilation rate and assimilate accumulation (Hu 2013). Moreover, Wang *et al*. (2015) treated tea crabapple (*Malus hupehensis*) seedlings with exogenous phlorizin, phloretin, cinnamic acid, p-hydroxybenzoic acid, and phloroglucinol and found that the total Chl and carotenoid (Car) contents of the leaves decreased after treatments. Moreover, net photosynthetic rate (P_N), stomatal conductance (g_s), and water-use efficiency (WUE) of the leaves were lower than the control values to varying degrees. Further analysis revealed that the phenolic acids might have destroyed chloroplasts in the leaves, thereby reducing the Chl content and inhibiting electron transport between Q_A and Q_B, leading to a decreased photosynthetic rate. Allelochemicals also inhibited maximum quantum yield of PSII primary photochemistry (F_v/F_m), ETR, and photosynthetic pigment contents in fern leaves, and the inhibitory effect was more evident with an increasing allelochemical content (Zhang *et al.* 2016).

The effect of phenolic acids on plants is a hot topic in allelopathy research. Despite reports concerning the effect of phenolic acids on plant photosynthesis (Yang *et al.* 2002; Blum *et al.* 2005), it is unclear how different phenolic acids affect the function of the photosynthetic apparatus and thus interfere with the transport rate of photosynthetic electrons between PSII and PSI. According to HPLC method, our preliminary experimental results showed that SA and PA exhibited a significant difference in different years of continuous cropping soil. Therefore, in this study, we investigated the response of photosynthetic parameters in strawberry seedlings to different concentrations of exogenous PA and SA and attempted to clarify the mechanism underlying the effect of phenolic acids on the photosystem functions and photosynthetic ETR in strawberry leaves. The results could provide reference data for an in-depth study regarding the soil sickness mechanism for strawberry.

Materials and methods

Experimental material: The experiment was conducted at the fruit tree experimental base of Shenyang Agricultural University (41º82'N, 123º57'E, Shenyang, Liaoning Province, China) from April to September in 2015. The daily average temperature was 23–28°C, the moisture contents of the soil were maintained at 70% of the field water-holding capacity, which could prevent the plants from drought stress. Seedlings of the strawberry (*Fragaria* × *ananassa* Duch.) of the cultivar 'Hokowase' were provided by the strawberry seedling production base of the Guobang Horticulture Farm in the Shenbei New District, Shenyang. Exogenous phenolic acids were purchased from *Sigma* (*Sigma Chemical Co.,* St. Louis, MO, USA).

Treatments: We prepared PA and SA solutions at gradient concentrations with a 0.3% ethanol solution as the solvent according to types and contents of phenolic acids detected in the rhizosphere of strawberry under continuous cropping conditions. Four concentrations were used to simulate phenolic acids accumulated in the soil during continuous strawberry cropping. SA and PA with the index of 1, 2, 3, and 4 represented the concentration of 1.0, 3.0, 9.0, and 27.0 μg g^{-1}, respectively. CK is normal management with water.

In April 2015, refrigerated strawberry heeled-in seedlings with four exterior leaves and one interior leaf were transplanted into plastic pots (upper diameter of 20 cm, lower diameter of 16 cm, and height of 30 cm). Each pot was filled with 2.0 kg of common garden soil. Each treatment was performed in a single-plant plot with 30 replications. After 20 d of rejuvenation, the plants were treated with exogenous phenolic acids by continuous irrigation with the prepared solutions (100 mL per plant) five times at 1-d intervals. Nine days after treatment, samples were collected to measure the relevant parameters. The pot experiment was performed in a greenhouse. The same amount of water and nutrients was supplemented regularly to ensure normal growth of the strawberry plants. Other management conditions were consistent.

Measurements: The Chl contents of strawberry leaves were measured according to the method described by Li (2006). After treatments with exogenous phenolic acids, fresh leaves were cut into pieces (removing the midrib). A *CIRAS-2* portable photosynthesis system (*PP-Systems,* USA) was used to measure the photosynthetic parameters of fully expanded functional leaves in the center of palmately compound leaves after 10 d of phenolic acid treatment. A stable adjustable source of gas was provided by the CO_2 cylinder equipped with the photosynthesis system, and the CO_2 concentration was controlled at 380 μmol mol^{-1}. The PAR was set to 1,200 μmol(photon) m^{-2} s^{-1} using an LED light source. PAR, air temperature, leaf temperature, vapour pressure, relative humidity, and other parameters were controlled using the automatic control system of the instrument. The P_N, g_s, intercellular CO_2 concentration (C_i), and WUE were measured at 9:00–11:00 h on sunny days.

An *M-PEA* multi-function plant efficiency analyser (*Hansatech,* United Kingdom) was used to measure the Chl fluorescence parameters of functional strawberry leaves following the method of Schansker *et al.* (2003). After full dark adaptation (30 min), the leaves were exposed to saturation pulse light [3,000 μmol(photon) m^{-2} s^{-1}] for 1 s. The parameter values were automatically recorded by the instrument. The following fluorescence parameters were obtained using *Biolyzer 4.0* software:

Relative variable fluorescence at the K-step (W_k):
$W_k = V_k/V_j = (F_k - F_o)/(F_j - F_o)$;
Relative variable fluorescence at the J-step (V_j):
$V_j = (F_j - F_o)/(F_m - F_o)$;
Performance index on absorption basis (PI_{ABS}):
$PI_{ABS} = (RC/ABS)\,[\Phi_{Po}/(1 - \Phi_{Po})]\,[\Psi_o/(1 - \Psi_o)]$;
$F_v/F_m = 1 - (F_o/F_m) = \Phi_{Po}$

The value of RC/ABS, Φ_{Po}, and Ψ_o can be calculated by the *M-PEA* directly.

The modulated reflection of PSI at 820 nm (MR/MR_0) was measured to reflect the redox state of the Chl *a* maximum absorption peak of molecules at 700 nm (P_{700}) by determining the decrease in the maximum amplitude decreased far red light (Munekage *et al.* 2004, Zhang *et al.* 2011). MR/MR_0 maximal slope descending (V_{PSI}) and MR/MR_0 maximal slope increasing ($V_{PSI+\ PSII}$) were used to indicate the redox capacity of PSI. V_{PSI} was calculated from the falling slope of MR/MR_0 in the range of 0.7–3 ms; $V_{PSI+\ PSII}$ was calculated from the maximum rising slope of MR/MR_0 in the range of 7–300 ms (Sun *et al.* 2015).

Data analysis: The data were analysed by one-way analysis of variance (*ANOVA*) using *DPS 7.05*. The significance of the differences was determined by *Duncan*'s multiple range test at the significance level $P<0.05$. The data calculations were performed using *Excel 2010*. Graphs were drawn using *Sigma Plot 10.0*.

Results

Leaf pigments: Application of exogenous SA (S1–S4) and PA (P1–P4) had a significant effect on photosynthetic pigment synthesis in the strawberry leaves (Table 1). After the SA treatment, all four SA concentrations inhibited photosynthetic pigment synthesis in the leaves; the inhibitory effect was enhanced by increasing the SA concentration. The Chl *a*, Chl *b*, Chl (*a*+*b*), and Car contents of the strawberry leaves decreased by 25.8, 28.6, 26.6, and 12.0%, respectively, after the S4 treatment compared with the control. However, with the exception of S1, the treatments resulted in markedly higher ratio of Chl *a*/*b* than that of the control. Different from the SA treatment, PA promoted the photosynthetic pigment contents in strawberry leaves at low concentrations and inhibited at high concentrations. The treatment with low PA concentrations (P1 and P2) increased the Chl *a*, Chl *b*, Chl (*a*+*b*), and Car contents; in particular, the Chl *a* content increased by 14.4 and 12.4%, respectively, compared with the control. In contrast, the high PA concentrations (P3 and P4) reduced the Chl *a*, Chl *b*, Chl (*a*+*b*), and Car contents. Significantly higher Chl *a*/*b* values were observed for the PA treatments compared with the control and SA treatments, indicating that the two phenolic acids had a stronger inhibitory effect on Chl *b*.

Photosynthetic parameters: Treatments with all four concentrations of exogenous SA significantly decreased the P_N, g_s, C_i, and WUE in the strawberry leaves compared with the control (Fig. 1). P_N, g_s, and WUE exhibited a constantly decreasing trend with the increasing SA concentration. In particular, P_N declined by 16.9, 32.6, 44.9, and 50.6% compared with the control values, and significant differences were observed between S1–S4 concentrations. Similarly, the exogenous PA treatment

Table 1. Effects of exogenous phenolic acids on photosynthetic pigment contents of strawberry leaves. Values are means of five replicates ± SD. Different *lowercase letters* in the same column indicate significant difference at 0.05 level. SA – syringic acid; PA – phthalic acid; 1, 2, 3, and 4 represent the concentrations of 1.0, 3.0, 9.0, and 27.0 μg g^{-1}, respectively. CK – normal management with water; Chl – chlorophyll; Chl *a*/*b* – the ratio of Chl *a* and Chl *b*.

Treatment	Chl *a* [mg g^{-1}(FM)]	Chl *b* [mg g^{-1}(FM)]	Chl (*a*+*b*) [mg g^{-1}(FM)]	Chl *a*/*b*	Carotenoids [mg g^{-1}(FM)]
CK	0.97 ± 0.03^{ab}	0.42 ± 0.04^{ab}	1.39 ± 0.03^{b}	2.31 ± 0.04^{c}	0.25 ± 0.01^{a}
SA1	0.91 ± 0.08^{ab}	0.40 ± 0.02^{ab}	1.31 ± 0.10^{bc}	2.28 ± 0.05^{c}	0.30 ± 0.02^{a}
SA2	0.88 ± 0.01^{ab}	0.36 ± 0.01^{ab}	1.24 ± 0.02^{b}	2.44 ± 0.05^{abc}	0.29 ± 0.01^{a}
SA3	0.81 ± 0.05^{ab}	0.33 ± 0.05^{ab}	1.14 ± 0.05^{de}	2.46 ± 0.08^{abc}	0.25 ± 0.02^{a}
SA4	0.72 ± 0.14^{b}	0.30 ± 0.04^{b}	1.02 ± 0.18^{e}	2.40 ± 0.08^{bc}	0.22 ± 0.03^{a}
PA1	1.11 ± 0.08^{a}	0.45 ± 0.02^{a}	1.56 ± 0.10^{a}	2.47 ± 0.05^{abc}	0.27 ± 0.02^{a}
PA2	1.09 ± 0.01^{a}	0.44 ± 0.01^{a}	1.53 ± 0.02^{a}	2.45 ± 0.05^{abc}	0.26 ± 0.01^{a}
PA3	0.92 ± 0.05^{ab}	0.35 ± 0.05^{ab}	1.27 ± 0.05^{bcd}	2.63 ± 0.08^{ab}	0.22 ± 0.02^{a}
PA4	0.87 ± 0.14^{ab}	0.32 ± 0.04^{ab}	1.19 ± 0.18^{cd}	2.72 ± 0.08^{a}	0.24 ± 0.03^{a}

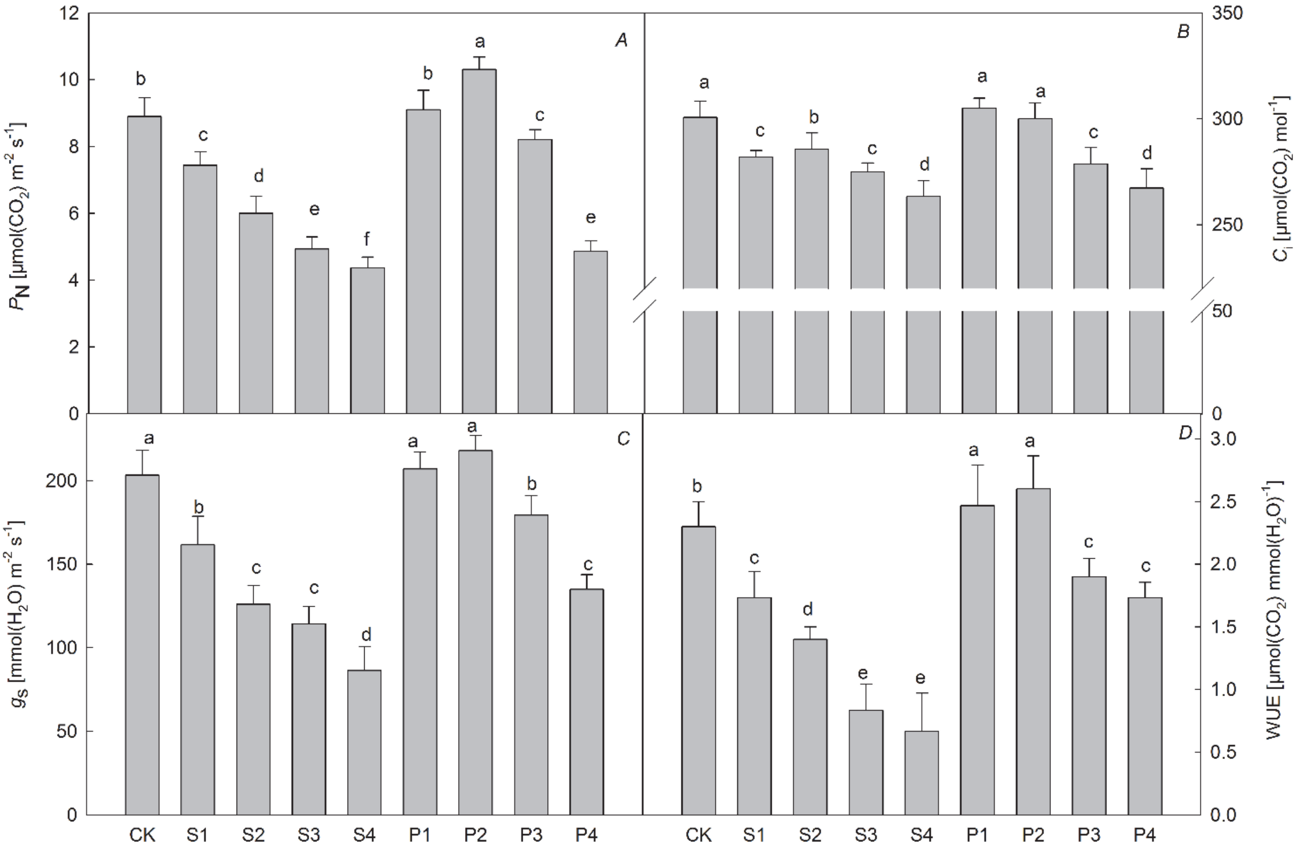

Fig. 1. Effects of exogenous phenolic acids treatments on photosynthetic parameters of strawberry leaves. S – syringic acid; P – phthalic acid; 1, 2, 3, and 4 represent the concentrations of 1.0, 3.0, 9.0, and 27.0 μg g^{-1}, respectively. CK – normal management with water, C_i – intercellular CO_2 concentration, g_s – stomatal conductance, P_N – net photosynthetic rate, WUE – water-use efficiency.

stimulated the photosynthetic parameters of strawberry leaves at low concentrations and inhibited at high concentrations. The treatment with the low PA concentrations (P1 and P2) did not significantly increase the P_N, g_s, C_i, or WUE; however, the treatment with the high PA concentrations (P3 and P4) significantly decreased the tested photosynthetic parameters and the P_N values of the P3 and P4 treatments accounted for 92.1 and 55.1% of the control, respectively. The effects of phenolic acids on the photosynthetic parameters were closely related to the type and concentration of phenolic acids.

Chl fluorescence induction curves: A deformation occurred in the curves of Chl fluorescence induction dynamics in strawberry leaves treated with exogenous phenolic acids (Fig. 2*A*). After the leaves were exposed to the saturation pulse, the overall trend of the curves was consistent for the different phenolic acid concentrations. However, there were certain differences in the fluorescence intensity of the induction curves, especially between the J phase (2 ms) and I phase (30 ms). Moreover, the modulated reflection curves at 820 nm (reflecting the redox capacity of PSI) showed certain differences between different exogenous phenolic acid treatments and the control (Fig. 2*B*), suggesting that exogenous phenolic acids might reduce the PSI redox activity in the strawberry leaves. The phenolic acid affected the PSI and PSII function which resulted in changes of the Chl fluorescence induction kinetics and modulated the reflection curve at 820 nm.

PSII Chl fluorescence characteristics: The W_k indicates the activity of OEC and V_j reflects the PSII acceptor side (electron transported from Q_A to Q_B). V_j and the W_k exhibited an upward trend in strawberry leaves with increasing concentrations of exogenous phenolic acids compared with the control (Table 2). After the treatment with the high phenolic acid concentrations, compared with CK, S4 fluorescence parameters increased by 28.8% in V_j and 100% in W_k. However, the P4 fluorescence parameters were enhanced by 21.2% in V_j and 69.2% in W_k compared with the control values.

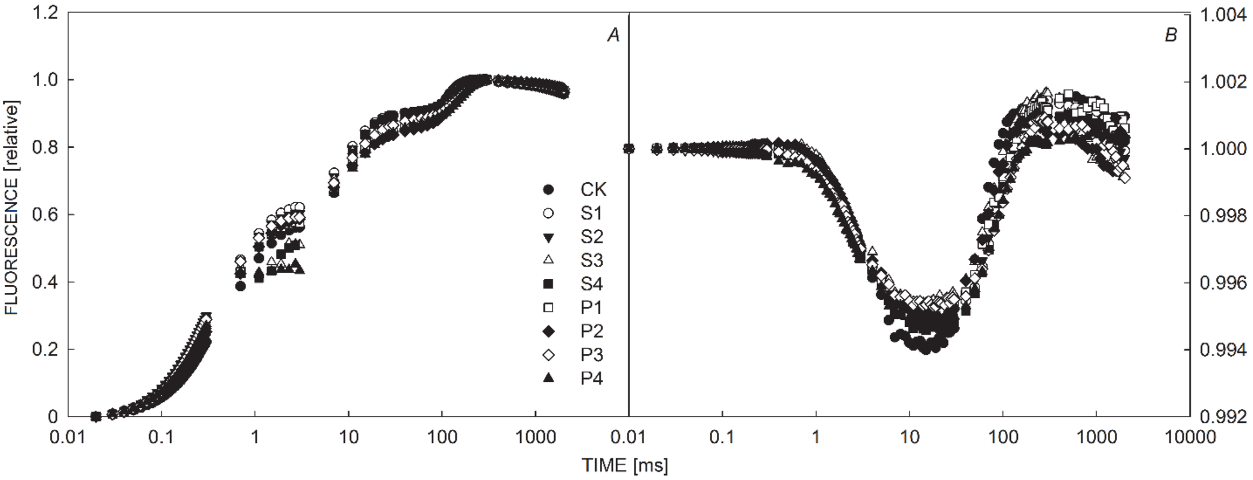

Fig. 2. Effects of exogenousphenolic acids treatments on fluorescence induction kinetics of strawberry leaves. S – syringic acid; P – phthalic acid; 1, 2, 3, and 4 represent the concentrations of 1.0 $\mu g \cdot g^{-1}$, 3.0 $\mu g \cdot g^{-1}$, 9.0 $\mu g \cdot g^{-1}$, and 27.0 $\mu g \cdot g^{-1}$, respectively. CK – normal management with water.

Table 2. Effect of exogenous phenolic acids treatments on chlorophyll fluorescence parameters in strawberry leaves. Values are means of five replicates ± SD. Different *lowercase letters* in the same column indicate significant difference at 0.05 level, SA – syringic acid; PA – phthalic acid; 1, 2, 3, and 4 represent the concentrations of 1.0, 3.0, 9.0, and 27.0 $\mu g\ g^{-1}$, respectively. CK – normal management with water. P_N – the net photosynthetic rate; F_v/F_m – the maximum quantum yield of PSII primary photochemistry; PI_{ABS} – the performance index on absorption basis; W_k – the relative variable fluorescence at the K-step; V_j – the relative variable fluorescence at the J-step; V_{PSI} – MR/MR_0 maximal slope descending; $V_{PSI+PSII}$ – MR/MR_0 maximal slope increasing.

Treatment	F_v/F_m	V_j	W_k	PI_{ABS}	V_{PSI}	$V_{PSI+PSII}$
CK	0.82 ± 0.02^{ab}	0.52 ± 0.02^{bc}	0.26 ± 0.01^{d}	2.46 ± 0.05^{c}	0.00210 ± 0.00002^{c}	0.00520 ± 0.00009^{a}
SA1	0.78 ± 0.02^{bc}	0.53 ± 0.03^{bc}	0.31 ± 0.02^{bcd}	2.09 ± 0.19^{d}	0.00210 ± 0.00003^{c}	0.00390 ± 0.00005^{b}
SA2	0.74 ± 0.01^{cd}	0.57 ± 0.03^{ab}	0.38 ± 0.02^{bcd}	1.84 ± 0.06^{e}	0.00250 ± 0.00003^{bc}	0.00380 ± 0.00004^{b}
SA3	0.70 ± 0.02^{d}	0.60 ± 0.04^{ab}	0.40 ± 0.04^{abc}	1.51 ± 0.09^{f}	0.00290 ± 0.00004^{ab}	0.00210 ± 0.00007^{c}
SA4	0.68 ± 0.01^{d}	0.67 ± 0.01^{a}	0.52 ± 0.01^{a}	1.16 ± 0.09^{d}	0.00310 ± 0.00001^{a}	0.00180 ± 0.00006^{c}
PA1	0.85 ± 0.01^{ab}	0.51 ± 0.01^{bc}	0.28 ± 0.01^{cd}	2.69 ± 0.08^{b}	0.00220 ± 0.00001^{c}	0.00530 ± 0.00002^{a}
PA2	0.87 ± 0.01^{a}	0.43 ± 0.05^{c}	0.29 ± 0.02^{cd}	2.97 ± 0.23^{a}	0.00210 ± 0.00005^{c}	0.00380 ± 0.00012^{b}
PA3	0.74 ± 0.02^{cd}	0.58 ± 0.02^{ab}	0.41 ± 0.03^{abc}	2.20 ± 0.09^{d}	0.0020 ± 0.00002^{c}	0.00360 ± 0.00018^{b}
PA4	0.70 ± 0.01^{d}	0.63 ± 0.03^{ab}	0.44 ± 0.02^{ab}	1.68 ± 0.07^{ef}	0.00190 ± 0.00003^{c}	0.00360 ± 0.00009^{b}

The F_v/F_m values of the strawberry leaves increased by 3.3 and 5.4% after the P1 and P2 treatments, respectively, compared with the control; however, the other phenolic acid treatments resulted in lower F_v/F_m values than that of the control. The most significant decrease in the F_v/F_m was observed after the S4 treatment, which only accounted for 82.9% of the control. The PI_{ABS} reflects the overall performance of PSII in plant leaves. With the increasing concentration of exogenous SA, the PI_{ABS} of the strawberry leaves showed a downward trend, with 85.1, 75.1, 61.3, and 47.3% decreases in S1–S4, respectively, relative to the control values. After the treatment with the low PA concentrations, PI_{ABS} increased by 9.3 and 20.7% in P1–P2, while the treatment with the high PA concentrations this parameter was markedly decreased by 10.6 and 31.7% in P3–P4 compared with the control (Table 2). The study showed that treatment with different phenolic acid concentrations could impair both the donor side of OEC and acceptor side Q_A of PSII in the strawberry leaves, which significantly inhibited the overall function of PSII and ultimately affected the transport rate of photosynthetic electrons in the electron transport chain. The effect of exogenous SA was greater than that of PA on PSII functions in strawberry leaves, and this negative effect was more significant under higher concentrations.

PSI Chl fluorescence characteristics: V_{PSI}, which is a fluorescence parameter indicating the redox capacity of PSI, exhibited an upward trend with increasing concentration of SA (Table 2). The values significantly increased by 38.1 and 47.6% for the S3 and S4 treatments, respectively, compared with the control. However, $V_{PSI+PSII}$ exhibited a clear downward trend at the slow-rising phase of MR/MR_0. There was no significant difference in V_{PSI} following treatment with different exogenous PA concentrations compared with the control. With the exception of the P1 treatment, the $V_{PSI+PSII}$ exhibited a slight downward trend for the PA treatment concentrations. The study showed that exogenous phenolic acid treatments could affect the overall redox capacity of the PSI in strawberry leaves. The effect of SA treatment was more significant than that of PA treatment, and the effect was dependent on the treatment concentration.

Discussion

Obstacles to continuous cropping can lead to total crop destruction and have serious adverse consequences for the healthy development of the strawberry industry. One of the main obstacles to continuous cropping is the accumulation of phenolic acids.

Significant positive effects of low PA concentrations on Chl *a*, Chl *b*, total Chl, and Car contents were observed in the present study, whereas the synthesis of photosynthetic pigments in strawberry seedlings were significantly inhibited at higher concentrations. These promoting effects at low concentrations and inhibiting effects at high concentrations are similar to those reported by Hu *et al.* (2013). However, SA treatments inhibited the synthesis of photosynthetic pigments in strawberry seedlings, and this inhibitory effect was gradually enhanced with the increasing SA concentration, similarly to the effect of phenolic acids on Chl accumulation in rice (Yang 2002).

Many studies have demonstrated that chemical substances can affect photosynthesis in plants as well as other physiological and biochemical processes (Einhelling *et al.* 1995). Chemical substances can affect photosynthesis directly by affecting not only stomatal factors, such as E, g_s, and C_i, but also by nonstomatal factors, such as photosynthetic pigments. According to Einhelling *et al.* (1979), phenolic acids, such as ferulic acid and caffeic acid, can inhibit plant growth by reducing photosynthesis, Chl content, and g_s in leaves. The results of the present study suggest that g_s, P_N, and C_i were enhanced at low concentrations of PA and inhibited at high concentrations. We showed that the allelochemicals permeated through the plant after treatment with high concentrations of PA, which destroyed the photosynthetic apparatus and inhibited photosynthesis and growth. By contrast, low concentrations of PA (4 g g^{-1}) might enhance E and supply CO_2 in mesophyll cells by improving the stomatal opening in strawberry leaves, resulting in an increase in P_N, and promoting accumulation of assimilation products. Various indexes generally showed an inhibitory effect of SA, including on the P_N and E. The decrease in g_s was significantly greater with the increasing SA concentration compared to increasing PA concentration, but there was no obvious difference in C_i, which indicated that photosynthesis was limited by nonstomatal factors in strawberry. This study also showed that phenolic acid treatment had no significant effect on Chl fluorescence parameters at low concentrations (4 μg g^{-1}) but significantly reduced the photochemical quenching coefficient in strawberry seedlings, resulting in decrease in F_v/F_m to different degrees at high concentrations (27 μg g^{-1}). Therefore, both types of phenolic acid treatments can decrease primary light energy conversion by PSII and ETR at high concentrations. This decrease reduced the production of ATP and the rate of carbon assimilation, thus affecting the accumulation of strawberry assimilation products and reducing the strawberry biomass.

The PI_{ABS}, which can sensitively reflect the overall function of the photosynthetic apparatus in plants, is an important indicator for the photoinhibition of PSII under abiotic stress (Yu 2006). In our experiment, both types of phenolic acids caused a decrease in the F_v/F_m and PI_{ABS} in strawberry leaves, thereby impairing the function of the entire PSII. However, the resulting excitation energy was transported from PSII to PSI through plastocyanin, which might impair the PSI functions to some extent. As the concentration of exogenous phenolic acids increased, the P_{700} content, which was indicative of the PSI redox reaction, showed a significant downward trend. According to the changes in $V_{PSI+PSII}$, the ETR from PSII to P_{700} in an oxidation state excited by red light was significantly decreased. As shown by the changes in V_{PSI}, the independent oxidation-reduction rate of P_{700} increased before the electrons were transported from PSII to PSI by treatments with the increasing phenolic acid concentrations. The degradation of the antenna pigment in PSI was slower than the degradation of P_{700} in the reaction centre, possibly because the phenolic acids affected the ratio of the antenna pigment to the PSI reaction centre pigment. The significant decrease in PSI activity could be attributable to PSI impairment. Another possible explanation is that the PSII acceptor side was seriously impaired and failed to supply electrons to PSI normally, leading to unsynchronized degradation of the antenna pigment and the PSII and PSI reaction centre pigments. Consequently, the PSI and PSII activities markedly declined and the coordination of PSI and PSII was damaged, thereby affecting the normal transport of photosynthetic electrons. The treatment with low phenolic acid concentrations did not seriously impair the photosynthetic apparatus, and the PSII and PSI functions appeared to be in a normal state. In summary, impairment of either PSI or PSII could affect the functions of the entire photosynthetic apparatus, resulting in a decrease in the photosynthetic efficiency and biomass. However, which photosystem was impaired more seriously under phenolic acid stress and the critical sites of action by phenolic acids are still unclear and are the focus of our next study.

Conclusion: Exogenous phenolic acids decreased the photosynthetic pigment contents, altered the composition of photosynthetic pigments, and affected the photosynthetic capacity of strawberry leaves. High exogenous phenolic acid concentrations impaired the donor and acceptor sides of PSII, thereby affecting ETR. Furthermore, this change caused a reduction in the redox capacity of PSI and therefore affected the overall function and ETR of the photosystems, leading to a decrease in the carbon assimilation ability in the leaves. Exogenous SA treatment exhibited a stronger effect than that of PA treatment.

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