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Low concentrations of $NaHSO_3$ increase photosynthesis, biomass, and attenuate photoinhibition in Satsuma mandarin (*Citrus unshiu* Marc.) plants

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Abstract

Spraying low concentrated (0.5–5.0 mM) solutions of $NaHSO_3$ on Satsuma mandarin (*Citrus unshiu* Marc.) leaves resulted in enhancement (maximal about 15 % at 1 mM $NaHSO_3$) of net photosynthetic rate (P_N) for 6 d. The potential photochemical efficiency of photosystem 2 (PS2, F_v/F_m) and the quantum yield of PS2 electron transport (Φ_{PS2}) were increased under strong photon flux density (PFD). The slow phase of millisecond delayed light emission (ms-DLE) was increased, showing that the transmembrane proton motive force related to photophosphorylation was enhanced. We also observed that low concentrations of $NaHSO_3$ promoted the production of ATP in irradiated leaves. We suggest that the increase in P_N in Satsuma mandarin leaves caused by low concentrations of $NaHSO_3$ solution may have been due to the stimulation of photophosphorylation and, hence, the increase in photochemical efficiency through speeding-up of PS2 electron transport. Photoinhibition of photosynthesis in leaves was modified by $NaHSO_3$ treatment under high PFD. Hence the increase in leaf dry mass seems to be associated with the mitigation of photoinhibition caused by strong PFD.

Additional key words: chlorophyll fluorescence; delayed light emission; $NaHSO_3$; photophosphorylation; photosynthetic CO_2 assimilation; photosystem 2.

Introduction

Sulphur dioxide (SO_2) is a noxious industrial and, occasionally, a natural atmospheric pollutant. Under normal physiological pH, bisulfite (HSO_3^-) is the major form of dissolved SO_2 in water (Puckett *et al*. 1973, Pfanz *et al*. 1987). Many authors have reported the injurious effects of bisulfite (or SO_2) on photosynthetic process (Asada *et al*. 1968, Hill 1974, Daniell and Sarojini 1981).

Zelitch (1957, 1966) found by *in vitro* experiments that α-hydroxysulfonates were specific inhibitors of glycolic acid oxidase and bisulfite had similar effect. He suggested that the effect of bisulfite was due to the formation of α-hydroxysulfonate by the reaction between $NaHSO_3$ and acetaldehyde acid (Zelitch 1957). Several years later, he observed that photosynthesis was enhanced and photorespiration was inhibited in tobacco leaf disks by the treatment with α-hydroxysulfonate (Zelitch 1966). Yin *et al*. (1979), Shen *et al*. (1980), and Wang *et al*. (2000a,b) sprayed low concentrations of bisulfite on the leaves of rice, wheat, and cotton, and found that it increased P_N for several days. Similar results were also demonstrated in higher plants by Katainen *et al*. (1987) who found that P_N of pine seedlings was markedly higher after exposure to SO_2 for couples of days, and Baxter *et al*. (1989) also observed that P_N in *Sphagnum* was significantly stimulated by 0.1 μmol m^{-3} bisulfite. However, the authors did not attach to these findings and have never tested its application to fruit trees.

Black and Unsworth (1979) observed an increase in P_N of *Vicia faba* leaves after exposure to low concentration of SO_2 for several minutes, together with an increase in stomatal opening. However, Menser and Heggestad (1966) reported a decrease in stomatal aperture with such treatment in spite of increase in P_N. Zhang and Peng (1984) attributed the stimulating effect of $NaHSO_3$ on P_N to its inhibitory effect on photorespiration. However, Tan and Shen (1987) showed that treating plants with low concentrations of HSO_3^- had no suppressing effect on photorespiration while photosynthesis was increased by

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Abbreviations: Chl – chlorophyll; *E* – transpiration rate; F_0 – minimal fluorescence; F_m – maximal fluorescence; F_v – variable fluorescence; F_v/F_m – photochemical efficiency of PS2; FM – fresh mass; g_s – stomatal conductance; ms-DLE – ms-delayed light emission; PFD – photon flux density; P_N – net photosynthetic rate; PS – photosystem; Φ_{PS2} – quantum efficiency of PS2.
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such treatment. A thorough investigation concurring the causes of enhancing effect of $NaHSO_3$ on P_N is necessary, which will contribute to elucidation of the theoretical basis of spraying $NaHSO_3$ as a measure of increasing agricultural production.

Irradiation is the ultimate energy source whose deficit inevitably limits photosynthesis. However, the exposure of plants to a high PFD can cause a depression of photosynthesis and photosystem 2 (PS2) efficiency, and even photodamage (Long *et al*. 1994). This decrease in P_N induced by high PFD is called photoinhibition (Adir *et al*. 2003). With shade treatment, photoinhibition of citrus trees can be reduced in field conditions (Raveh *et al*. 2003), however, it is arduous to control PFD due to its changeability in field. Therefore, we need to explore the possibility of using a simple technique to reduce photoinhibition and promote photosynthesis.

Citrus is the most important fruit tree in China. Its P_N is lower than that in crops under natural conditions (Chen *et al*. 1994). The aim of this work was to study the influence of low concentrations of $NaHSO_3$ on Satsuma mandarin P_N, photoinhibition, and biomass.

Materials and methods

Plant: Two-year-old Satsuma mandarin (*Citrus unshiu* Marc.) plants were grown in large plastic pots (35 cm in diameter, 35 cm tall) in a phytotron where the day/night temperature was 25/20 °C, the relative humidity was 60–70 %, and the PFD was about 700–800 μmol m^{-2} s^{-1}. The soil in the pots was composed of loam, peat, and coarse sand in a ratio 7 : 3 : 2 (v : v). Four plants or more per treatment were used in the following experiments.

$NaHSO_3$ treatment: A microsprayer was used to spray water (as control) or $NaHSO_3$ solutions of different concentrations on mature leaves. Furthermore, the plants were sprayed with a solution of 1 mM $NaHSO_3$, with a six-day interval for 90 d.

Biomass: At the end of the experiment, the treated and control plant leaves were separately plucked, dried at 80 °C for 48 h, and dry mass of leaves was measured. Before desiccation, leaf area was measured with a leaf measurement system (*LI-3000*, *LI-COR*, Lincoln, NE, USA). The biomass was calculated as the ratio of the dry mass to leaf area.

Strong irradiance treatment: The mature leaves of plants were sprayed with 1 mM $NaHSO_3$ three times at 40 min intervals within 2 h on a sunny day, and then exposed to strong PFD of 1 800 μmol m^{-2} s^{-1} for 3 h the next day. The actinic radiation from four 400 W dysprosium lamps was allowed to pass through an 8-cm layer of flowing water between the lamps and the leaves to remove heat.

Gas exchange: Net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were measured according to Guo *et al*. (2005) with an open system (*HCM–1000*, *Walz*, Effeltrich, Germany) under an artificial irradiance source of dysprosium lamps, using the fifth completely expanded leaf from the top of each plant, at a temperature of 25 °C under a saturating irradiance of 800 μmol m^{-1} s^{-1} , relative humidity 45 %, and CO_2 concentration of 350 μmol mol^{-1}. Leaf temperature was controlled by using a leaf cuvette with a temperature control system (*1010-M*, *Walz*, Effeltrich, Germany). Photosynthetic response to irradiance was studied with PFD of about 0 to 1 200 μmol m^{-2} s^{-1} at the level of measured leaves.

Chlorophylls (Chls) were extracted with 80 % acetone and assayed according to Porra *et al*. (1989).

Chl fluorescence of the leaves was measured at room temperature (25 °C) with a portable fluorometer (*PAM-2000*, *Walz*, Germany) after the leaves were dark-adapted for 2 h. The fluorometer was connected to a trifurcated fiber-optic (*2010-F*) and to a computer with data acquisition software (*PAMWin 1.03*). The experimental protocol of Genty *et al*. (1989) was basically followed. The minimal fluorescence (F_0) with all PS2 reaction centres open was measured with modulated irradiance which was sufficiently low (<0.1 μmol m^{-2} s^{-1}) not to induce significant variable fluorescence (F_v). The maximal fluorescence (F_m) with all PS2 reaction centres closed was determined by a 0.8 s saturating pulse at 8 000 μmol m^{-2} s^{-1} in dark-adapted leaves. Then, the leaves were continuously irradiated with "white actinic light" (536 μmol m^{-2} s^{-1}). The steady state value of fluorescence (F_s) was thereafter recorded and a second saturating pulse at 8 000 μmol m^{-2} s^{-1} was imposed to determine maximal fluorescence in the light-adapted state (F_m'). The actual quantum yield of PS2 photochemistry $\Phi_{PS2} = (F'_m - F_s)/F_m'$ was calculated as defined by Genty *et al*. (1989).

Ms-DLE of the treated and control leaves was measured according to the procedure of Li and Shen (1994) with a laboratory-made phosphoroscope. A sample in a polymethylmethacrylate cuvette was treated by radiation passing through a 2 cm-thick layer. The holes on the rotating wheels were arranged so that the measuring process may have been divided into the series of 5.6-ms cycles for the excitation measurement, *i.e.* 1 ms excitation by the irradiance (1 500 μmol m^{-2} s^{-1}) followed by 4.6-ms darkness. The delayed irradiance between 2.8 and 3.8 ms after every flash was measured with an *EMI9558B* photomultiplier with a red glass filter. The signal passing through an amplifier was recorded continuously by *Sc-16* light beam oscillograph.

ATP content was measured according to Ronner *et al*. (1999) with slight modifications. Bilaterally symmetrical Satsuma mandarin leaves were selected. After removal of middle vein, discs of equal area were cut and then kept in

boiling water for 10 min. ATP content in the solutions was measured with luciferin-luciferase assay. The medium for measurement contained 50 mM glycylglycine (pH 7.6), 10 mM $MgSO_4$, and 1 M EDTA.

Statistical analysis: All measurements were made between 08:00 and 11:00 and replicated at least six times. The data were subjected to analysis of variance (*ANOVA*) and the significance of the Duncan's multiple range test at p=0.05 level using *SPSS*.

Results

After treating the leaves with different concentrations of $NaHSO_3$ in the morning, the P_N was measured the next morning (Table 1). 0.5 to 5.0 mM $NaHSO_3$ significantly increased P_N of the leaves, but an inhibitive effect appeared when $NaHSO_3$ concentration exceeded 10 mM. The optimum concentration of $NaHSO_3$ for promoting P_N in citrus was 1 μmol m^{-3}. No significant differences between the treated and control leaves in g_s and E were observed.

The time-course of P_N in leaves treated with 1 mM $NaHSO_3$ was recorded. Fig. 1*A* shows that the enhancement of photosynthetic assimilation in treated leaves was maintained for 6 d. The treated plants had higher maximal values of P_N on a leaf area basis than the control plants (Fig. 1*B*).

There was no significant difference in Chl content and ratio of Chl *a/b* between the treated and control leaves (Table 2).

After being sprayed with 1 mM $NaHSO_3$ solution, the potential photochemical efficiency of PS2 (F_v/F_m) and the quantum yield of PS2 electron transport (Φ_{PS2}) of the leaves were higher than those of the control leaves

Table 1. Effect of different concentrations of $NaHSO_3$ on net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) of the leaves of Satsuma mandarin. Means ± SE (n = 6). Different letters indicate significant differences by the Duncan's multiple range test at p=0.05.

Photosynthetic parameter	$NaHSO_3$ concentration [mM]					
	0 (control)	0.5	1.0	2.0	5.0	10.0
P_N [μmol m^{-2} s^{-1}]	6.7±0.3 c	7.1±0.2 b	8.2±0.5 a	8.0±0.4 a	7.3±0.2 b	5.4±0.5 d
g_s [mmol m^{-2} s^{-1}]	75.5±7.4 a	77.4±6.3 a	78.3±8.5 a	74.3±6.9 a	75.8±9.1 a	72.2±8.3 a
E [mmol m^{-2} s^{-1}]	1.1±0.1 a	1.1±0.1 a	1.1±0.1 a	1.0±0.1 a	1.01±0.1 a	1.0±0.1 a

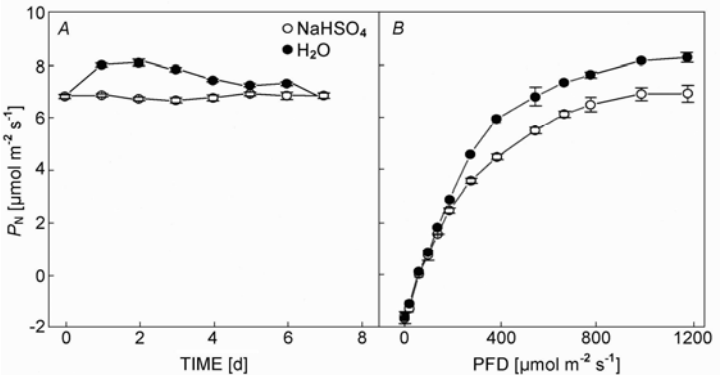

Fig. 1. Time progress (*A*) and irradiance response (*B*) of P_N of the Satsuma mandarin leaves treated with 1 mM $NaHSO_3$. Means ± SE of six (*A*) or three (*B*) replications.

(Table 3), but the minimal fluorescence (F_0) was not significantly different from the control. The changes in F_m and the F_v/F_m in $NaHSO_3$ treated and control leaves were examined after exposure to different PFD. The F_m and F_v/F_m decreased with increasing PFD (data not shown), but the $NaHSO_3$ treated leaves still maintained values about 10−15 % higher than the control leaves under PFD of 800 μmol m^{-2} s^{-1}.

We indicated (Li and Shen 1993) that the ATP formed by photophosphorylation was not always sufficient for carbon assimilation and could have been a limiting factor in photosynthesis. An enhancement of P_N stimulated by the proton motive force provides the energy for overcoming the activation barrier of the recombination process. Wraight and Crofts (1971) studied the effect of different components of the proton motive force on the ms-DLE with uncouplers and concluded that the fast phase of ms-DLE correlated with rapid $NaHSO_3$ increases brought about increased ATP production during photophosphorylation. ATP content of the irradiated leaves should be also increased. Our results showed that the leaves treated with 1 mM $NaHSO_3$ had higher amount of ATP than control (Table 2).

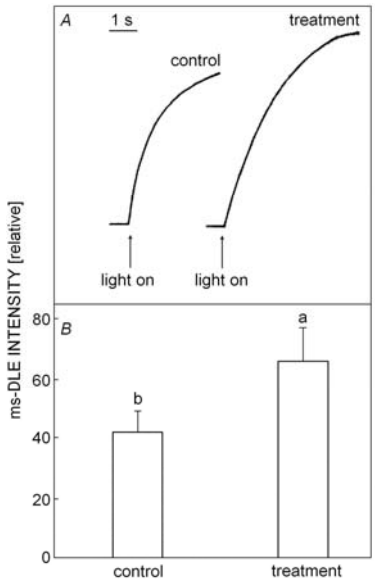

Fig. 2. The effect of $NaHSO_3$ on the relative intensity of ms-DLE of Satsuma mandarin leaves treated with 1 mM $NaHSO_3$. *Each column with bar* indicating SE represents the mean of 4 separate experiments. *Different letters on column* indicate significant differences at p=0.05 using *ANOVA* followed by the Duncan's multiple range test. *A*: Induction curves of ms-DLE recorded with light beam oscillograph. *B*: Relative intensity of ms-DLE.

Table 2. Chlorophyll (Chl) content, ratio of Chl *a/b*, ATP content, and leaf dry mass in the Satsuma mandarin leaves after being treated with 1 mM $NaHSO_3$. Means ± SE (n = 6). The values for treatment and control indicated with the letter a were not significantly different at p=0.05 using *ANOVA* followed by the Duncan's multiple range test.

Parameter	Control	Treatment
Chl (*a*+*b*) [g kg^{-1}(FM)]	3.10±0.13 a	3.12±0.11 a
Chl *a*/*b*	3.05±0.02 a	3.04±0.04 a
ATP content [μmol kg^{-1}(FM)]	0.33±0.05 b	0.39±0.13 a
Leaf dry mass [kg m^{-2}]	11.4±0.3 b	12.7±0.4 a

Millisecond delayed light emission (ms-DLE) of chloroplasts originates from the back reaction of irradiation-induced charge separation in PS2, which is establishment of the thylakoid membrane potential while the slow phase was stimulated mainly by a proton gradient across the thylakoid membrane. We indicated that $NaHSO_3$ treatment increased significantly the slow phase of ms-DLE, which reflects mainly transmembrane photon gradient that can drive photophosphorylation (Fig. 2).

The plants were initially sprayed with 1 mM $NaHSO_3$ solution and H_2O, respectively, and thereafter every six days until ninetieth day. Leaf dry mass was significantly increased in the treated plants after ninety days (Table 2).

Discussion

Treating the leaves with low concentration of $NaHSO_3$ as a measure to enhance P_N of wheat, rice, and other plants was widely tested in China (Shen *et al*. 1980, Tan and Shen 1987, Wang *et al*. 2000a,b), but there has been no report on the effect of $NaHSO_3$ on P_N in the evergreen plant citrus. We applied $NaHSO_3$ (0.5–5.0 mM) to leaves which caused an increase in P_N (Table 1), and the increased value was maintained for more than six days (Fig. 1).

There was no significant difference in Chl content between the control and treated plants, indicating that mechanism by which $NaHSO_3$ increases photosynthetic CO_2 assimilation was mainly due to its effect on operation of the photosynthetic apparatus (Table 2).

Besides the enhancement of P_N, 1 mM $NaHSO_3$ also increased ATP content of Satsuma mandarin leaves (Table 2). This fact seems to imply that the stimulation of P_N by low concentrations of $NaHSO_3$ was mainly due to increased production of ATP. Furthermore, $NaHSO_3$ treatment also significantly increased intensity of the slow phase ms-DLE reflecting mainly proton gradient across the thylakoid membrane (Fig. 2). Thus, the stimulation was due to transmembrane photon gradient that drives photophosphorylation.

Comparing the data of plants treated by $NaHSO_3$ with those of the control, F_v/F_m and Φ_{PS2} of the former were found to be higher (Table 3). We suggest that the increase in F_v/F_m of the Satsuma mandarin leaves caused by low concentrations of $NaHSO_3$ solution may have been due to the stimulation of photophosphorylation, and hence the increase in PS2 electron transport.

Photoinhibition occurs when photons absorbed by the photosynthetic apparatus are in excess of the amount used by photosynthesis, which is characterized by the decline in F_v/F_m and apparent quantum yield of O_2 evolution or CO_2 uptake (Long *et al*. 1994). Previously we reported that photoinhibition occurred in citrus leaves under strong PFD (Guo *et al*. 1999, Song *et al*. 2003). We found that after being sprayed with 1 mM $NaHSO_3$ solution, the

Table 3. Effects of $NaHSO_3$ on the fluorescence parameters of Satsuma mandarin leaves. Means ± SE (n = 6). The values for treatment and control indicated with letters a and b were significantly different at p=0.05 using *ANOVA* followed by the Duncan's multiple range test.

Plants	Chlorophyll fluorescence parameters [relative]			
	F_0	F_m	F_v/F_m	Φ_{PS2}
Control	0.318±0.003 a	1.313±0.052 b	0.764±0.006 b	0.608±0.006 b
Treated	0.314±0.003 a	1.424±0.061 a	0.807±0.006 a	0.674±0.009 a

value of F_v/F_m of leaves showed a significant increase, probably due to the effect of $NaHSO_3$ on alleviation of photoinhibition (Table 3).

In conclusion, fruit crop citrus Satsuma mandarin showed a general response to $NaHSO_3$ treatment as reported for other crops, *i.e.* wheat, rice, and other plants treated by $NaHSO_3$ (Wang *et al*. 2000a,b). The increase in biomass caused by $NaHSO_3$ treatment was mainly due to an increase in P_N and a mitigated photoinhibition.

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