Plant Growth Regulation (2006) 48:65–72
DOI 10.1007/s10725-005-4403-z

Different pathways are involved in the enhancement of photosynthetic rate by sodium bisulfite and benzyladenine, a case study with strawberry (*Fragaria*×*ananassa Duch*) plants

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Received 1 February 2005; accepted in revised form 21 October 2005

Key words: Benzyladenine (BA), Gas exchange, Millisecond delayed light mission, Sodium bisulfite ($NaHSO_3$), Strawberry

Abstract

In order to understand the pathway involved in the chemical enhancement of photosynthetic rate, sodium bisulfite ($NaHSO_3$) and benzyladenine (BA), a growth regulator, were applied to strawberry plants. The influence of these compounds on gas exchange and millisecond delayed light emission (ms-DLE) was investigated using 2-month-old plants. Results showed the net photosynthetic rate (A) in leaves was promoted by both $NaHSO_3$ and BA. Stomatal conductance (g) and transpiration rate (E) were significantly increased only by BA, while intercellular CO_2 concentration (C_i) was significantly decreased by $NaHSO_3$. The enhancement of A by $NaHSO_3$ and BA was only a short-term effect, lasting approximately 5 days for $NaHSO_3$ and 30 h for BA. Plants treated with $NaHSO_3$, BA or $NaHSO_3$ + BA, showed no significant fluctuations in carboxylation efficiency (CE), photorespiration (R_P) or dark respiration (R_D). These results suggest that the influences of $NaHSO_3$ and BA on gas exchange particularly A, could be via different mechanisms: the enhancement of A by the application of low concentrations of $NaHSO_3$ appears to be associated with increased cyclic electron flow, while BA enhancement of A is at least partially due to increased g and/or E.

Abbreviations: A – net photosynthetic rate; BA – benzyladenine; CE – carboxylation efficiency; C_i – intercellular CO_2 concentration; E – transpiration rate; g – stomatal conductance; P_R – photo-respiratory rate; R_D – rate of dark respiration; $NaHSO_3$ – sodium bisulfite; ms-DLE – millisecond delayed light emission

Introduction

Bisulfite (HSO_3^-), a physiological form of SO_2, is generally considered to be detrimental to plant tissues (Daniell and Sarojini 1981; Zoran et al. 1982). Previous work has shown that bisulfite can have adverse effects on the photosynthetic process (Asada 1968; Hill 1974; Ziegler 1975; Daniell and Sarojini 1981). However, Shen et al. reported that photosynthesis in cyanobacteria could be enhanced by the application of low concentrations (20–200 μmol l^{-1}) of $NaHSO_3$ (Wang et al. 2003a), an observation that has also been recorded for some field crops (Tan and Shen 1987; Wang et al. 2000a, b; Wang and Shen 2002; Guo et al. 2003; Zhou et al. 2003). Similar results were also found for pine seedlings where *A* was markedly higher for 2 days after exposure to SO_2 (Katainen et al. 1987).

Cytokinins play a number of critical roles in plant growth and development, in particular the regulation of chlorophyll concentration and the delay of leaf senescence (Binns 1994). Application of the cytokinin benzyladenine (BA) has been shown to increase both the number of chloroplasts per cell (Nii and Kuroiwa 1986) and chlorophyll concentration (Walker et al. 1988). In strawberry plants, BA has been used to stimulate runner production (Prits et al. 1986). Although exogenously applied cytokinins are known to increase *g*, *E* and *A*, these results are considered to be species and concentration dependent (Pospíšilová et al. 2001; Pospíšilová 2003; Vomacka and Pospisilova 2003).

It is generally accepted that the cyclic electron transport around photosystem I (PSI) requires ATP and NADPH (Slovacek et al. 1978; Gerst et al. 1995). Numerous investigations have shown that, in addition to the direct measurement of redox change of P700 (Asada et al. 1993), the level of cyclic electron transport can be estimated from the intensity of the millisecond delayed light emission (ms-DLE) originating from Photosystem II (PSII). Generally, ms-DLE can be divided into two phases. In the first, designated the fast phase, a sharp rise in signal appears within 0.1 s of the start of flashing light illumination. The slow phase follows within a few seconds, and is marked by a change in the signal as it reaches and maintains a steady state. Crofts and colleagues (Wraight and Crofts 1971; Evans and Crofts 1973; Bowes et al. 1979) have shown that the fast phase of ms-DLE is associated with a rapid establishment of the thylakoid membrane potential, while the slow phase of ms-DLE was stimulated mainly by a proton gradient across the thylakoid membrane.

The mechanism by which SO_2 or bisulfite stimulates photosynthesis still remains obscure. Wang et al. (2003a, b) proposed that bisulfite at lower concentrations (1–2 mmol l^{-1}) increased the *A* of wheat and rice by accelerating cyclic electron flow around PSI. But, others (Gao et al. 1981; Zhang and Pang 1984) have attributed the stimulatory effect of bisulfite on *A* to the inhibition of photorespiration (Zelitch 1966). The above discrepancy prompts further study to examine the effect of bisulfite application on the behavior of cyclic electron flow on the ms-DLE.

Despite numerous reports of $NaHSO_3$ enhancing *A* in a number of species (Ferguson and Lee 1979; Katainen et al. 1987; Baxter et al. 1989; Wang et al. 2000a), and of BA enhancing of gas exchange (for review see Pospíšilová 2003), there is no report of the combined effects of $NaHSO_3$ and BA on gas exchange in the strawberry. The objectives of the study were 2-fold. The first was to investigate the effects of applied $NaHSO_3$, BA, or a combination of the two, on *A* in strawberry, and the second was specifically to compare the mechanisms, especially the process related to the cyclic electron flow, by which the two chemicals promote *A*.

Materials and methods

Plant material

Two-month-old strawberry plants (*Fragaria*×*ananassa* Duch. cv. Fengxiang) were transferred into pots (15×20 cm^2, diameter×height) filled with soil and organic compost. One plant was placed in each pot, after which the pots were arranged in five rows with 40 cm between rows and 30 cm between the pots.

The pots were placed in a greenhouse where temperatures ranged between 20 and 30 °C under natural photoperiod. Plants were regularly watered and fertilized as required.

Sodium bisulfite and benzyladenine treatments

$NaHSO_3$ solutions at concentrations of 0.5, 1, 2, 5, 10 mmol l^{-1} plus a distilled water control, were applied on three occasions at 3 h intervals when the plants had 8–9 leaves. Solutions of BA were applied once at concentrations of 0.2, 1, 2, 10 μmol l^{-1}. Solutions were applied with a hand-held pressurized sprayer until run-off (about 10 ml). To determine the duration of an effect, we selected 1 mmol l^{-1} $NaHSO_3$ or 2 μmol l^{-1} BA as optimal concentration after comparing the effect of different concentrations of these chemicals on *A*. Gas exchange parameters were measured 24 h after the application of 1 mmol l^{-1} $NaHSO_3$, and then daily over a 6-day period, or at 3-h interval following BA application over a 33-h period.

Plants were divided into treatment groups following a completely randomized design. There were at least 10 plants within each treatment. After the spray applications, six randomly selected plants from each treatment group were used for the measurement of gas exchange parameters.

Measurements of photosynthetic gas exchange

Net photosynthetic rate (*A*), transpiration rate (*E*), stomatal conductance (*g*) and intercellular CO_2 concentration (C_i) were measured according to Guo et al. (2005) with an open gas exchange system (HCM-1000, Walz, Effeltrich, Germany) under an artificial light source of four 400 W dysprosium lamps (above an 8 cm layer of water acting as a heat sink). Measurements were made on the fifth completely expanded leaf of each strawberry plant, at a temperature of 25 °C in a leaf chamber under a photosynthetic photon flux density (PPFD) of 700 μmol m^{-1} s^{-1}, relative humidity of 45%, and CO_2 concentration of 380 μmol mol^{-1}.

Photorespiration (P_R) and dark respiration (R_D) were measured according to the procedure described by Xu et al. (2004). Carboxylation efficiency (CE) of leaves was measured according to Von Cammerer and Farquhar (1981) at a PPFD of 700 μmol m^{-2} s^{-1}.

All measurements were made between 8:00 and 11:00 a.m. and were replicated at least three times.

Measurement of millisecond delayed light emission (ms-DLE)

Measurements of ms-DLE were undertaken with laboratory made equipment according to the procedure described by Li and Shen (1994). The signal was detected with a lab-made phosphoroscope. The sample of leaf was placed in a polymethylmethacrylate cuvette and irradiated with light passing through the 2 cm-thick wall. The holes on the rotating wheels were arranged so that measurement could be divided into a series of 5.6 ms cycles for the excitation measurement (i.e., 1 ms excitation by 1500 μmol m^{-2} s^{-1} of light) followed by 4.6 ms of darkness. The delayed light between 2.8 and 3.8 ms after every flash was measured with an EMI9558B photomultiplier with a red glass filter. The signal was amplified and recorded continuously with a Sc-16 light beam oscillograph.

Statistical analysis

All of the data were subjected to analysis of variance (ANOVA). The significance of the Tukey test was determined at a 5% level (Zar 1984).

Results

Determination of optimal levels of $NaHSO_3$ and BA via effects on gas exchange parameters

The effects of $NaHSO_3$ and BA on leaf gas exchange parameters are shown in Table 1. These results indicate that *A* was enhanced by the application of low concentrations (0.5, 1.0, 2.0 mmol l^{-1}) of $NaHSO_3$, but inhibited at higher concentrations of $NaHSO_3$ (5.0, 10.0 mmol l^{-1}). In addition, it was determined that the optimum concentration of $NaHSO_3$ for enhancement of *A* in strawberry was 1 mmol l^{-1}, which significantly increased *A*. While C_i was significantly depressed at low concentrations (0.5, 1.0, 2.0, 5 mmol l^{-1}) of $NaHSO_3$, but not at 10.0 mmol l^{-1} $NaHSO_3$. In contrast, there were no significant effects of $NaHSO_3$ on *E* or *g* in any treatment.

E and *g* were significantly increased by BA at all concentrations, except at 10 μmol l^{-1} BA (Table 1). For *A*, there was a significant increase only at 2.0 μmol l^{-1} BA, i.e. *A* by 17% compared

Table 1. Effects of $NaHSO_3$ and BA applications at a range of concentrations on leaf gas exchange in strawberry.

Treatment		A (μmol CO_2 m^{-2} s^{-1})	g (mmol H_2O m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	C_i (μmol mol^{-1})
$NaHSO_3$ (mmol l^{-1})	0.	11.3 ± 0.6 b	136 ± 12 a	3.62 ± 0.61 a	236 ± 15 a
	0.5	13.3 ± 0.6 ab	137 ± 12 a	3.64 ± 0.43 a	214 ± 14 ab
	1.0	14.5 ± 0.2 a	141 ± 16 a	4.26 ± 0.64 a	202 ± 12 b
	2.0	13.4 ± 0.5 ab	137 ± 12 a	4.21 ± 0.54 a	218 ± 15 ab
	5.0	11.6 ± 0.6 b	135 ± 17 a	3.73 ± 0.20 a	200 ± 18 b
	10.0	10.5 ± 0.4 c	133 ± 10 a	3.68 ± 0.27 a	246 ± 19 a
BA (μmol l^{-1})	0 .0	11.9 ± 0.7 b	116 ± 5 b	3.14 ± 0.13 b	233 ± 17 a
	0.2	12.1 ± 0.3 ab	130 ± 5 ab	3.66 ± 0.09 a	225 ± 16 a
	1.0	12.2 ± 0.5 ab	137 ± 6 ab	3.74 ± 0.11 a	221 ± 18 a
	2.0	13.8 ± 0.4 a	149 ± 4 a	3.93 ± 0.09 a	219 ± 22 a
	10.0	12.6 ± 0.5 ab	122 ± 7 b	3.39 ± 0.27 b	220 ± 14 a

Note: Means within each column that are followed by the same letters are not significantly different according to the Tukey test ($p < 0.05$). Data are presented as the mean ± standard error ($n = 6$).
$NaHSO_3$ was applied three times in consecutive 3-h intervals before gas exchange parameters were measured 24 h after application. BA was applied once, and gas exchange parameters were measured 3 h after application.

to the control. No changes in C_i were observed with any BA treatment relative to the control.

Effects of $NaHSO_3$ and BA over time on A, g, E and C_i

Figure 1 shows the effect of 1 mmol l^{-1} $NaHSO_3$ on A, g, E and C_i 6 days after application. Results indicate that the effect of $NaHSO_3$ on gas exchange occurred around 6 days. The significant promotive effect of $NaHSO_3$ on A was observed 1–3 days after application and declined by day 4 after application. A similar timeframe was observed with the decrease in C_i after application of $NaHSO_3$. However, g and E were not influenced by 1 mmol l^{-1} $NaHSO_3$.

The effects of 2 μmol l^{-1} BA on A, g, E and C_i are shown in Figure 2. The greatest enhancement of A was observed 6–9 h after BA application. This subsequently declined during the remainder of the experiment (about 21 h). Significant enhancements of g and E were observed 3 h after the application of 2 μmol l^{-1} BA, before a sharp decline in both parameters. C_i was only slightly influenced by BA application.

Effects of a combined application of $NaHSO_3$ and BA on gas exchange parameters, R_D, P_R and CE

Table 2 shows the combined effects of an application of 1 mmol l^{-1} $NaHSO_3$ and 2 μmol l^{-1} BA on gas exchange parameters, R_D, P_R and CE. The results showed that there was a significant enhancement of A compared to the control. Meanwhile, g and E were also significantly increased with the application of 2 μmol l^{-1} BA, or in combination with 1 mmol l^{-1} $NaHSO_3$, but not with 1 mmol l^{-1} $NaHSO_3$ alone. C_i was significantly decreased by 1 mmol l^{-1} $NaHSO_3$, or in combination with 2 μmol l^{-1} BA, but not by 2 μmol l^{-1} BA alone.

In general, there was no significant influence on R_D, P_R and CE with the application of 1 mmol l^{-1} $NaHSO_3$, 2 μmol l^{-1} BA or $NaHSO_3$ + BA. However, a clear decline in R_D and P_R after $NaHSO_3$ application was observed, although it was not significant compared to the control. The 2 μmol l^{-1} of BA appeared to increase P_R and inhibit R_D in the experiment. CE was not significantly influenced by either chemical alone or by the combination of the two.

Treatment with $NaHSO_3$ + BA produced no significant difference in any of the tested parameters when compared to BA alone (Table 2).

Effects of $NaHSO_3$ and BA on ms-DLE

The intensity of ms-DLE was measured after application of $NaHSO_3$ and BA (Figure 3). The results indicated that the slow phase of ms-DLE was significantly increased by $NaHSO_3$, while the fast phase of ms-DLE was not significantly influenced by either $NaHSO_3$ or BA.

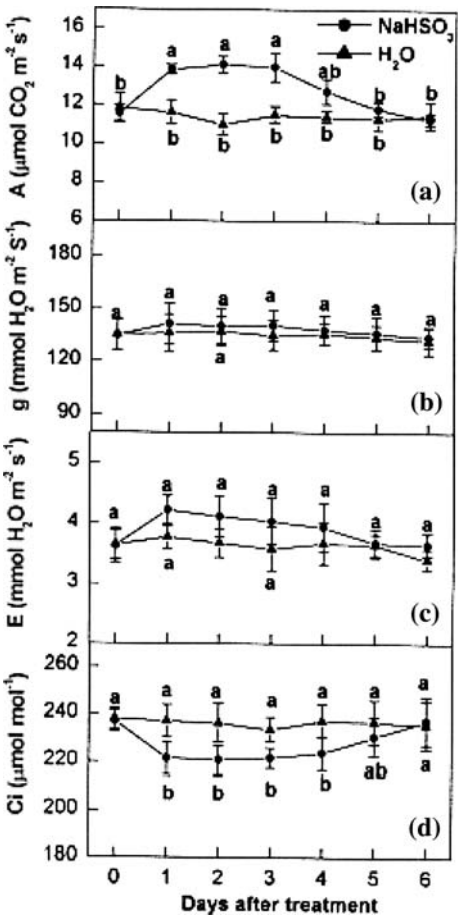

Figure 1. Time course of the effect of 1 mmol l^{-1} $NaHSO_3$ on A, g, E and C_i in strawberry leaves. $NaHSO_3$ was applied on three consecutive occasions at 3-h intervals. Means followed by the same letters are not significantly different according to the Tukey test ($p < 0.05$). Data are presented as the mean ± standard error ($n = 6$).

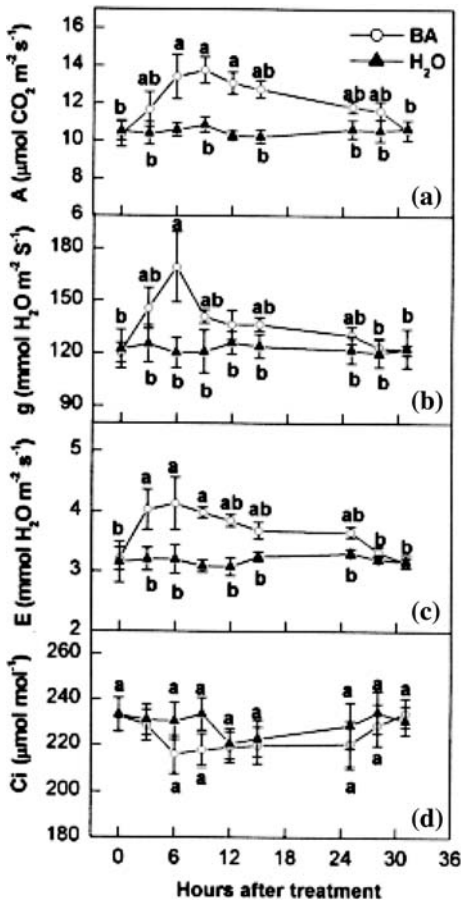

Figure 2. Time course of the effect of 2 μmol l^{-1} BA on A, g, E and C_i in strawberry leaves. BA was applied once. Means followed by the same letters are not significantly different according to the Tukey test ($p < 0.05$). Data are presented as the mean ± standard error ($n = 6$).

Discussion

Applications of $NaHSO_3$ and the growth regulator BA have been shown to enhance photosynthesis in a number of species (Ferguson and Lee 1979; Wang et al. 2000a, b; Wang et al. 2003a, b; Zhou et al. 2003). The possibility that $NaHSO_3$ promotes A through sulfur fertilization has been precluded since Na_2SO_4 had no influence on assimilation (Wang et al. 2003a). However, an experiment using the alga *Chlorella vulgaris* also found that carbon fixation and growth were increased by sulfite (below 1 mmol l^{-1}) even when there was no sulfur deficiency (Soldatini et al. 1978).

The results of our study show that gas exchange was apparently influenced by both $NaHSO_3$ and BA, though the plants exhibited different responses to $NaHSO_3$ and BA application. Low concentrations of $NaHSO_3$ (which had an optimum concentration of 1.0 mmol l^{-1}) significantly increased A and decreased C_i, but had no effect on E and g. These observations are consistent with previously reported data (Wang et al. 2000a, b; Guo et al. 2003; Wang et al. 2003a, b). BA caused a significant increase in A, g and E. However, no significant influence on C_i was observed with any of the BA concentrations applied. These results imply that the impact of $NaHSO_3$ and BA on gas exchange in strawberry may occur via different pathways. The enhancement of A in

Table 2. Effects of $NaHSO_3$ and BA applications on the gas exchange in strawberry leaves.

Treatments	A (μmol CO_2 m^{-2} s^{-1})	g (mmol H_2O m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	C_i (μmol mol^{-1})	R_D (μmol CO_2 m^{-2} s^{-1})	R_P (μmol CO_2 m^{-2} s^{-1})	CE (mol m^{-2} s^{-1})
CK	11.8 ± 0.8 c*	120 ± 8 b	3.04 ± 0.21 b	237 ± 16 a	1.16 ± 0.09 a	5.12 ± 0.33 a	0.083 ± 0.002 a
1 mmol l^{-1} $NaHSO_3$	14.3 ± 0.3 b	126 ± 6 b	3.16 ± 0.16 b	203 ± 12 b	1.00 ± 0.08 a	4.93 ± 0.50 a	0.083 ± 0.002 a
2 μmol l^{-1} BA	15.4 ± 0.5 a	142 ± 10 a	4.02 ± 0.17 a	229 ± 15 a	1.01 ± 0.05 a	5.65 ± 0.15 a	0.083 ± 0.003 a
T1	16.1 ± 0.7 a	142 ± 7 a	4.28 ± 0.24 a	201 ± 11 b	1.28 ± 0.12 a	5.27 ± 0.42 a	0.085 ± 0.003 a

Note: Means within each column that are followed by the same letters are not significantly different according to the Tukey test ($p < 0.05$). Data are presented as the mean ± standard error ($n = 6$).
$NaHSO_3$ was applied three times in consecutive 3-h intervals and gas exchange parameters were measured 24 h after application. BA was applied once, and gas exchange parameters were measured 3 h after application. T1 plants were treated with $NaHSO_3$, 24 h prior to the application of BA. Gas exchange parameters of the T1 group were measured 3 h after BA application.

$NaHSO_3$ treated plants may be associated with changes in mesophyllic activity (Wang and Shen 2002; Wang et al. 2003a). The mechanism underlying enhancement of A by BA, however, may be the result of increased g and/or E.

An enhancement of A by different routes is often reflected in change in C_i; here $NaHSO_3$ application reduced C_i but BA did not. As g was unchanged, the decrease in C_i apparent with $NaHSO_3$ treatment suggests that enhancement of mesophyllic activity is the primary cause for an increase in A in strawberry. In contrast, the consistency of C_i after BA treatment suggests that stomatal factors, rather than mesophyllic activity, are the cause for

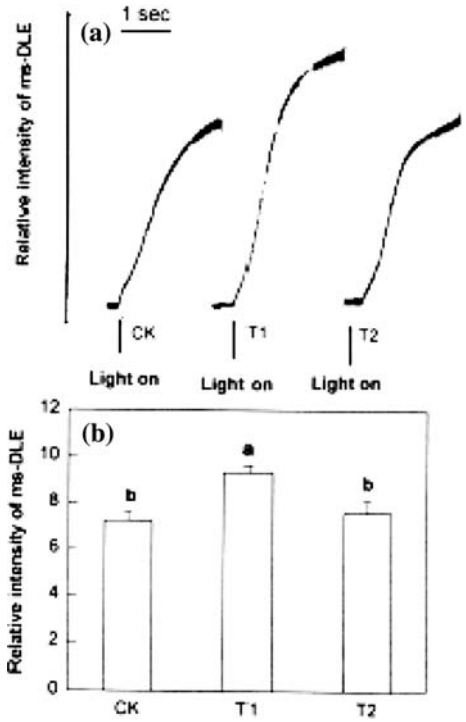

Figure 3. The effect of typical $NaHSO_3$ and BA application on millisecond delayed light emission (ms-DLE) in strawberry leaves. T1 plants were treated with 1 mmol l^{-1} $NaHSO_3$ three times in consecutive 3-h intervals and ms-DLE was measured after 24 h. T2 plants were treated with 2 μmol l^{-1} BA and ms-DLE was measured 3 h after application. Means followed by the same letters are not significantly different according to the Tukey test ($p < 0.05$). Data are presented as the mean ± standard error ($n = 6$). (a) Curves of ms-DLE recorded with light beam oscillograph. (b) Relative intensity of ms-DLE.

increased *A*. These findings are in accordance with the results in other plants (Pospíšilová et al. 2001; Pospíšilová 2003).

The role of $NaHSO_3$ in photosynthesis has been recognized by several researchers (Takemoto and Noble 1982; Zhang and Pang 1984), and it has been suggested to function by inhibiting photorespiration in crops such as rice, wheat and soybean (Gao et al. 1981). A significant inhibition in photorespiration by $NaHSO_3$ was not apparent in this study, which is in accordance with the report of Takemoto and Noble (1982). One explanation for this is that an increase in *A* by $NaHSO_3$ could be via an alternative pathway rather than through inhibition of photorespiration. Further experimentation showed that $NaHSO_3$ significantly increased the slow phase of ms-DLE, which primarily reflects the proton gradient across the thylakoid membrane, however there was little influence on Fv/Fm or any other chlorophyll fluorescence parameters (data not shown). The implication is that an enhancement of *A* by $NaHSO_3$ could be attributed to other mechanism.

Cyclic electron flow is believed to be linked to ATP production, which would compensate for any insufficient in the ATP supply utilized by carbon assimilation (Schürmann et al. 1972; Slovacek and Hind 1977; Mills et al. 1978; Slovacek et al. 1978). Cyclic electron flow is known to enhance the intensity of the ms-DLE (Wraight and Crofts 1971; Evans and Crofts 1973; Bowes et al. 1979). Therefore, changes in ms-DLE are thought to be indicative of the photophosphorylation-related transmembrane proton force (Wraight and Crofts 1971; Xu and Shen 1983). As the slow phase of ms-DLE was significantly promoted, suggesting that ATP supply through coupled photophosphorylation increased thereby enhancing cyclic electron flow around PSI, thus, *A* was enhanced (Xu et al. 1989; Guo et al. 1994).

Acknowledgements

The authors would like to thank Dr Kai Xu for providing the strawberry material. This work was supported by a Grant (No. 30471195) from National Natural Science Foundation of China.

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