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Enhancing ATP Formation to Increase Photosynthesis

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Introduction

ATP is the necessary component of assimilation power in photosynthesis. It is not only required for CO_2 assimilation but also for the maintaining of the operation of the photosynthetic apparatus, such as for the activation or PSP of several kinds of enzymes or other proteins. It is widely accepted that the reduction of $NADP^+$ by the photosynthetic noncyclic electron transfer is coupled with the formation of ATP. The ATP/NADPH ratio is generally considered to be 1.33, which is lower than the ratio required for the assimilation of one molecule of CO_2 to carbohydrate level. The insufficient amount of ATP is believed to be supplemented by cyclic or pseudocyclic PSP, though there is still debate about which way is more important (Shen and Wei 1998).

In our lab, we showed by several kinds of experiments that in many cases the photosynthesis was often limited by ATP supply, and might be enhanced by two kinds of means. One is to improve the coupling efficiency by some treatments, such as increasing the concentration of phosphate or polybasic acids, or adding some coupling efficiency improvers. The other way is to increase cyclic PSP by applying adequate amount of PMS solution to the leaves (Shen 1994).

Recently, we found that spraying 1-2 mmol L^{-1} of $NaHSO_3$ solution to the leaves could also enhance cyclic PSP *in vivo*, and thus increase photosynthesis. The main results in studying the underlying mechanism are reported here.

Materials and Methods

1.1 Wheat (*Triticum aestivum* L. var. J411) and spinach (*Spinacia oleracea*) were grown in the field of Shanghai Institute of Plant Physiology. Rice (*Oryza sativa* L. indica, var. Shanyou 63) and broad bean (*Vicia faba*) were grown in pots placed in phytotron of Shanghai Institute of Plant Physiology.

1.2 The net photosynthesis (Pn) of plant leaves was measured with portable gas exchange analyzer (CI-301, CID company, USA, for rice and broad bean, and LI-6400, LI-COR, Lincoln, USA, for wheat and spinach).

1.3 Measurement of ATP content in leaves was performed by luciferin-luciferase assay (Ronner et al 1999).

1.4 Millisecond delayed light emission of leaves was measured with a Becqurell type phosphoroscope (Xu and Shen 1984).

1.5 The transient increase of chlorophyll fluorescence after termination of the actinic light was measured with a PAM Chlorophyll Fluorometer (Mi et al 1995).

1.6 Measurement of redox change of P700 was performed using a PAM Chlorophyll Fluorometer (Walz, Effeltrich, Germany) with an emitter-detector-cuvette assembly (unit ED-P700DW-E) as described by Klughammer and Schreiber (1998).

2 Results and Discussion

2.1 Effect of treating plant leaves with $NaHSO_3$ on photosynthesis

In 1970's, we found that spraying $NaHSO_3$ on leaves of many plants could increase photosynthesis for several days (Shen et al 1980). These experiments can be repeated easily, and here are some of them that did recently (Table 1.).

Table 1. Effect of 1 mmol L^{-1} $NaHSO_3$ on Pn in attached leaves.

	Pn (μmol CO_2 m^{-2} s^{-1})	
	Control	$NaHSO_3$
Triticum aestivum(J411)	21.80±0.91	26.11±0.85
Oryza sativa L.(Shanyou 63)	25.72±1.37	30.44±0.77
Spinacia olerecea L.	15.17±0.28	18.61±1.28
Vicia faba	11.08±0.51	12.65±0.56

One or two years ago, it was ascertained that the cause of increasing photosynthesis by $NaHSO_3$ treatment was related to the effect that $NaHSO_3$ could enhancing ATP formation *in vivo,* which was indicated by raising ATP content in wheat and rice leaves under field conditions (Table 2.). When $NaHSO_3$ was sprayed on leaves during early stage of ripening, the grain yields were increased by 10.28±3.90% and 9.62±5.65% for wheat and rice respectively (Wang 2000a,b). Since $NaHSO_3$ is cheap and harmless at low concentration, it is hopeful to be used as a practical measure in agriculture production. Therefore, the mechanism of $NaHSO_3$ in enhancing ATP formation in leaves is worthy studying.

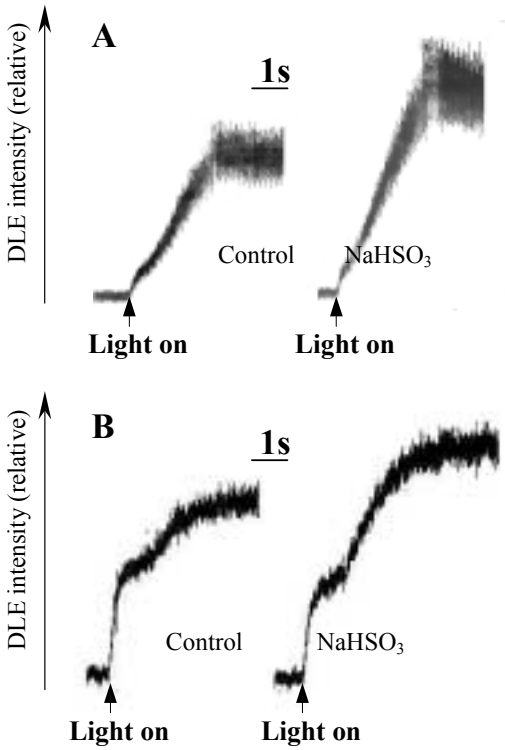

Fig. 1. Effect of 1 mmol L^{-1} $NaHSO_3$ on the millisecond delayed light emission of the flag leaves of rice Shanyou 63 (A) and wheat J411 (B).

2.2 Effect of $NaHSO_3$ on ms-DLE in leaves

The ms-DLE of chlorophyll from leaves reflects the intensity of transmembrane proton motive force, which is closely related to PSP (Shen et al 1998). The effect of $NaHSO_3$ on ms-DLE in wheat and rice leaves was shown in Fig 1. The results indicate that $NaHSO_3$ treatment significantly increased the slow phase of ms-DLE (which reflects mainly proton gradient across thylakoid membrane), and had little effect on the fast phase of ms-DLE (which reflects membrane electropotential and protons released from oxidation of water in PSII) (Xu and Shen 1984). It may be deduced that $NaHSO_3$ affected mainly the electron transport and the coupled PSP related to PSI but not PSII.

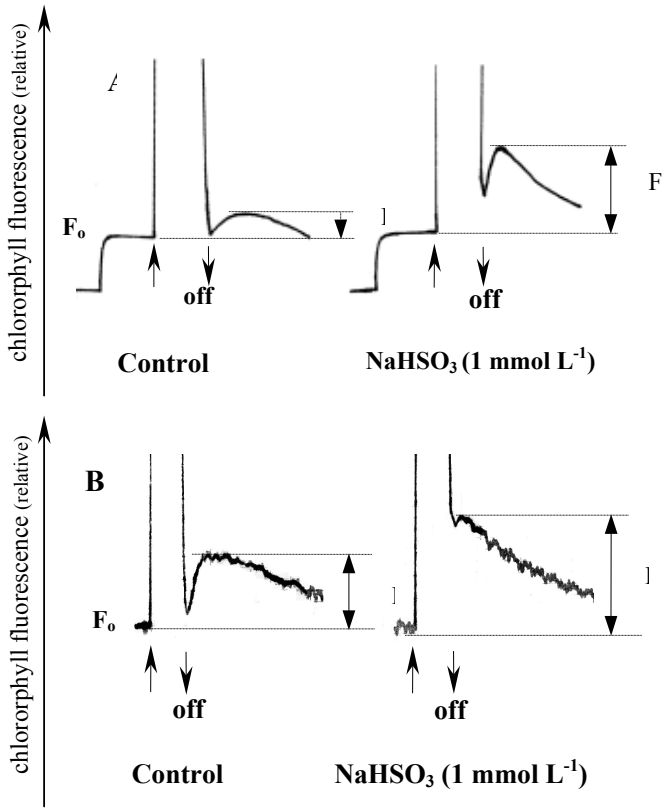

Fig. 2. Effect of 1 mmol L^{-1} $NaHSO_3$ on the post-illumination transient increase in chlorophyll fluorescence in leaves of rice Shanyou 63 (A) and wheat J411 (B).
AL, actinic light; Fp, height of post-illumination chlorophyll fluorescence peak.

2.3 Effect of $NaHSO_3$ treatment on the post-illumination transient increase in chlorophyll fluorescence in leaves

It was mathematically analyzed that change in magnitude of the post-illumination transient increase in chlo-rophyll fluorescence in leaves reflected the dynamic level of redox changes of PQ (Jin et al 2000). Treatment with 1 mmol L^{-1} of $NaHSO_3$ enhanced it (Fig.2), indicating that $NaHSO_3$ could enhance ATP formation by cyclic electron transport around PSI, which is in accordance with the ms-DLE experiment.

2.4 Effects of $NaHSO_3$ on the redox kinetics of P700 in leaves

Another new method to detect cyclic electron flow around PSI is to measure the half-time of P700 turnover (Schreiber et al 1988). After light activation, the dark reduction of P700 (PSI) following far-red light illumination was much accelerated by $NaHSO_3$ treatment in wheat J411 and rice Shanyou 63 leaves (Fig.3.). This showed a large increase in the number of electrons available to reduce $P700^+$ in the dark in leaves by 1 mmol L^{-1} of $NaHSO_3$, which from another aspect illustrate that the cyclic electron transport around PSI was enhanced by $NaHSO_3$ treatment.

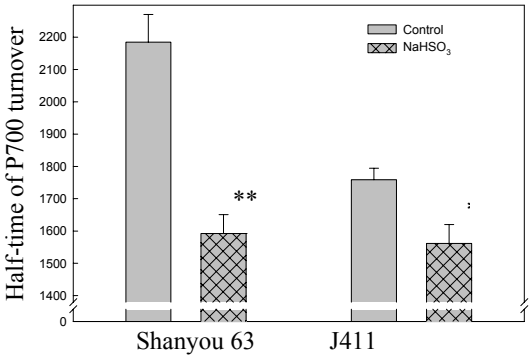

Fig. 3. Effects of 1 mmol L^{-1} $NaHSO_3$ on the redox kinetics of P700 in rice Shanyou 63 and wheat J411 leaves. The leaves were dark adapted before measurement. Each point is the mean with SE expressed as the length of the vertical bar. The significant levels of difference between control and treatment are indicated by asterisk *** and ** for $p < 0.001$ and $p < 0.01$, respectively.

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