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# Enhanced thermal energy dissipation depending on xanthophyll cycle and D1 protein turnover in iron-deficient maize leaves under high irradiance*

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## Abstract

Pigment contents of chloroplasts and net photosynthetic rate were dramatically reduced in maize leaves suffering from iron deficiency. However, the reduction in photosynthesis was probably not caused by decreased contents of chlorophylls and carotenoids and by photon absorption; the primary limiting factor for photosynthesis may rather be the decrease of electron transport activity in photosystem 1. Iron-deficient leaves suffered serious acceptor-side photoinhibition, and more than 60 % of absorbed photons were dissipated, while less than 40 % was used in photochemical reaction. Thermal energy dissipation depending on xanthophyll cycle and D1 protein turnover was enhanced when acceptor-side photoinhibition occurred in iron-deficient maize leaves.

*Additional key words*: carboxylation efficiency; carotenoids; chlorophyll; $CO_2$ concentration; fluorescence kinetics; energy dissipation; net photosynthetic rate; photosystems; *Zea mays.*

## Introduction

Iron is important in the synthesis of chlorophyll (Chl) in higher plants, and leaves suffering from iron deficiency show damaged chloroplast structure and decreased Chl content (Terry and Abadía 1986). As the Chl content decreases, the amount of absorbed excitation energy may decline, possibly leading to a decrease in the amount of excitation energy distributed to photochemical reaction. Iron is a constituent component of the photosynthetic electron transport chain: both photosystem (PS) 1 and PS2 complexes contain iron-proteins. The PS1 complex is particularly abundant in iron due to its four Fe-S proteins. The Fe-S protein synthesis is inhibited in iron-deficient leaves and the decreased size and activity of PS1 is attributed to the absence of this protein (Sandmann and Malkin 1983). The content of iron in PS2 is lower than that in PS1, but iron here plays a role in water splitting (Hulsebosch *et al.* 1996); thus also in PS2 the iron-deficiency may lead to decreased activity. Iron may play different roles in individual photosystems. The kind of damage of PS1 and PS2 caused by iron-deficiency may be different. If PS1 is damaged more seriously than PS2, acceptor-side photoinhibition is observed, whereas if PS2 is damaged more seriously, donor-side photoinhibiton is observed. Are the two kinds of photoinhibition associated with different energy dissipation mechanisms? If the activity of carbon assimilation decreases, more excess energy will result. Thus, the iron-deficient leaves will face greater risk of photodamage. Iron-deficiency may affect the photosynthetic apparatus in various ways. However, less information is available about how excitation energy may be distributed, and what is the main mechanism of energy dissipation that protects iron-deficient leaves against photodamage. Our objective was to gain a coherent understanding of the effects of iron-deficiency on photoprotection mechanisms.

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*Abbreviations*: A, antheraxanthin; $C_i$ – intracellular concentration of $CO_2$; Car, carotene; Chl, chlorophyll; D, fraction of photons absorbed in photosystem 2 antenna that is dissipated *via* thermal energy dissipation; DTT, 1,4-dithiothreitol; $F_v/F_m$, the maximal efficiency of photosystem 2 photochemistry in the dark-adapted state; $F_v'/F_m'$, efficiency of photosystem 2 units with open reaction centres during irradiation; NPQ, non-photochemical quenching; PFD, photon flux density; $P_N$, net photosynthetic rate; $P_{rate}$, photochemical reaction rate; pQ, plastoquinone; PS, photosystem; SM, streptomycin sulphite; V, violaxanthin; Z, zeaxanthin.

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## Materials and methods

**Plants**: The experiments were done in Tai-an city, Shandong Province, China, in July and August of 1999. Maize (*Zea mays* L.) plants (cv. Luyu11) were grown in Hoagland nutrient solutions with and without iron (iron was introduced into the medium as $FeSO_4$) under natural irradiation. The nutrient solutions of control and iron-deficient treatments were replaced 3 times a week and adjusted to pH 5.0±0.5 with HCl. After the plants had grown for 7 weeks, at which time serious symptoms of iron deficiency appeared, the youngest fully expanded leaves were used for measurements. Iron content of Hoagland nutrient solutions with and without iron measured by atomic absorption spectroscopy (*WFD-Y*, Japan) was 0.802 kg $m^{-3}$ in the control nutrient solution and undetected in iron-deficient nutrient solution, which indicated iron content less than 0.010 kg $m^{-3}$ in iron-deficient nutrient solution.

**Inhibitor treatments**: 6 mM DTT (1,4-dithiothreitol) was used to inhibit de-epoxidation of xanthophyll cycle (Park *et al.* 1995, Darkó *et al.* 2000, Xu *et al.* 2000, Ye *et al.* 2000). 2 mM SM (streptomycin sulphite) was used as an inhibitor of D1 protein synthesis (Leitsch *et al.* 1994, Schnettger *et al.* 1994, Darkó *et al.* 2000). Leaves were cut at the base of petiole and placed in a beaker containing water or solutions of inhibitors and kept under weak irradiance (10 µmol $m^{-2}$ $s^{-1}$) for 12 h.

**Net photosynthetic rate ($P_N$)**: $P_N$-PFD and $P_N$-$CO_2$ response curves were measured at room temperature (about 30 °C) with a portable photosynthetic system (*CIRAS-1, PP Systems*, UK). PFD was changed every 3 min in a sequence of 2 000, 1 600, 1 200, 800, 600, 400, 300, 200, 150, and 100 µmol $m^{-2}$ $s^{-1}$. $CO_2$ concentration was changed every 3 min in a sequence of 1 000, 800, 600, 400, 300, 200, 100, and 50 µmol $mol^{-1}$. Irradiance and $CO_2$ concentration were controlled by the automatic control function of the *CIRAS-1* photosynthetic system. Carboxylation efficiency was calculated according to the initial slope of $P_N$-$C_i$ response curve.

**Chl fluorescence parameters** were measured at room temperature with a portable fluorometer (*FMS2, Hansatech*, UK). Initial fluorescence ($F_0$) was recorded in leaves adapted to dark for 15 min. A single saturating radiation pulse was applied to obtain maximum fluorescence ($F_m$). Steady state fluorescence ($F_s$) was determined under actinic irradiation. The actinic irradiation was changed every 3 min in a sequence of 2 000, 1 200, 800, 600, 300, 100, and 0 µmol $m^{-2}$ $s^{-1}$. Saturating pulse was applied to obtain $F_m$' following each actinic irradiation. The actinic radiation was removed and the minimal fluorescence in the light-adapted state ($F_0$') was determined by irradiating the leaf disk for 3 s with far-red radiation.

The maximum efficiency of PS2 photochemistry in the dark-adapted state ($F_v/F_m$), efficiency of PS2 units with open PS2 reaction centres during irradiation ($F_v'/F_m'$), actual quantum yield of PS2 ($\Phi_{PS2}$) in the light-adapted state, non-photochemical quenching (NPQ), fraction of photons absorbed in PS2 antenna that is dissipated *via* thermal energy dissipation (D), and photochemical reaction rate ($P_{rate}$) were calculated using both light and dark fluorescence parameters according to Demmig-Adams *et al.* (1996).

**Pigment analysis**: Leaf Chls and carotenoids were extracted with 80 % acetone and the extracts were analysed using *UV-120* (*Shimadzu*, Japan) according to Arnon (1949). The carotenoids of xanthophyll cycle were determined according to Thayer and Björkman (1990) with some modifications. After dark adaptation for 12 h, leaves were exposed to irradiation of 1 200 µmol $m^{-2}$ $s^{-1}$ for 0, 0.5, 1, 2, or 3 h, then were quickly frozen in liquid nitrogen and extracted with 100 % acetone. Pigment separation was performed in an HPLC system (*Waters*, USA) at room temperature. The mobile phase was composed of three solvents: acetonitrile, methanol, and methylene chloride. To achieve a better separation of the xanthophyll cycle pigments, the elution program was as follows. During 0-10 min an 0.05 M mixture of solvents, acetonitrile – methanol – tris-HCl (75 : 15 : 10, v:v:v) was run, followed by 5 min of linear gradient, then the mixed solvent was changed to methanol and hexane (5 : 1) for 10 min. Between the two sample analyses, the column was re-equilibrated for 15 min with the mixed solvent used in the first period (0-10 min). The de-epoxidation of xanthophyll cycle was calculated in % using peak area:

$$(A + Z) = (A_{peak\ area} + Z_{peak\ area})/(V_{peak\ area} + A_{peak\ area} + Z_{peak\ area}).$$

Each experiment was conducted at least three times independently.

## Results

**Effect of iron deficiency on photosynthesis and pigment contents**: Remarkable difference in $P_N$ was observed in control and iron-deficient maize leaves (Fig. 1*A,B*): at iron deficiency $P_N$ increased very little by increasing PFD and $CO_2$ concentration. The saturating irradiances of control and iron-deficient maize leaves were about 1 600 and 300 μmol $m^{-2}$ $s^{-1}$, respectively, and the maximum $P_N$ under saturating PFD was about 35 and 1 μmol $m^{-2}$ $s^{-1}$, respectively. Maximum $P_N$ at saturating $CO_2$ of control and iron-deficient maize leaves were about 40 and 2 μmol $m^{-2}$ $s^{-1}$, respectively. The carboxylation efficiencies of iron-deficient and control leaves measured by the gas exchange method were 0.103 and 1.016, respectively (Fig. 1*C*).

One of the obvious characteristics of iron-deficient maize leaves was the reduction of Chl and carotenoid contents compared to control leaves (Table 1). However, the extent of decrease was significantly different among different pigments. In iron-deficient maize leaves, Chl *a* and Chl *b* contents decreased by about 90 %, while for carotenoids a decrease of only about 80 % was observed. The relative content of carotenoids was much higher in chlorotic Fe-deficient leaves compared to the control leaves (Table 1).

Table 1. Chlorophyll (Chl) and carotenoid (Car) contents [g $m^{-3}$] in control and iron-deficient (–Fe) maize leaves.

| | Chl *a* | Chl *b* | Car | Chl *a/b* | Car/Chl (*a* + *b*) |
|---|---|---|---|---|---|
| control | 17.63±2.80 | 4.77±1.60 | 5.07±1.50 | 3.69 | 0.23 |
| -Fe | 2.09±0.11 | 0.66±0.02 | 1.07±0.02 | 3.17 | 0.39 |

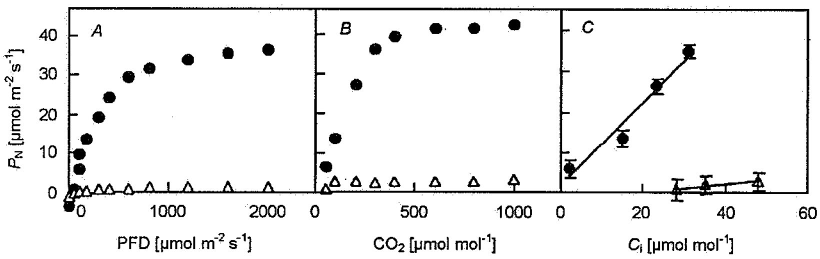

Fig. 1. Response curves of net photosynthetic rate ($P_N$) to irradiance (*A*) or $CO_2$ concentration (*B*), and carboxylation efficiency determined by the initial slope of $C_i$ response curve (*C*) in control (•) and iron-deficient (Δ) maize leaves measured in air (*A*) or at 1 200 μmol $m^{-2}$ $s^{-1}$ (*B*) at room temperature. Values in *C* are means ± SE of 3 separate experiments; for control y = 1.0158x + 2.0695, $r^2 = 0.9552$; for Fe-deficiency y = 0.0995x – 1.8487, $r^2 = 0.908$.

**Effects of iron deficiency on photosynthetic electron transport**: $F_v/F_m$ reflects the maximal PS2 efficiency when the reaction centres are fully opened, *i.e.*, when NPQ is absent. Thus $F_v/F_m$ may represent original activity of PS2 (Hulsebosch *et al.* 1996). $F_v/F_m$ in control and iron-deficient maize leaves was 0.85±0.03 and 0.75±0.02, respectively, thus it decreased by only 12 % due to iron-deficiency. Hence the PS2 integration and its function were not seriously harmed by the iron deficiency.

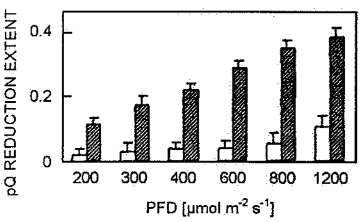

Fig. 2. Changes of pQ reduction extent in control (*empty columns*) and iron-deficient (*full columns*) maize leaves exposed to different PFD.

Because PS1 and carbon assimilation cycle are located behind PS2 along the electron transport chain, the extent of pQ reduction can be used to evaluate the relative activity of PS2 *versus* PS1/carbon assimilation cycle. If the activity of PS1 and carbon assimilation is lower than that of PS2, the electron transport behind PS2 is blocked and pQ reduction extent would be increased, whereas, if the activity of PS1 and carbon assimilation is higher than PS2, pQ reduction extent would be decreased. We found that pQ reduction extent in iron-deficient leaves was about 6 times higher than that in control leaves under weak and moderate irradiance, and only 4 times higher under high irradiance (Fig. 2). From these values we can deduce that the effect of iron deficiency on PS2 was less severe than that on PS1 and/or carbon assimilation.

**Effect of iron deficiency on excitation energy distribution**: The photochemical reaction rate ($P_{rate}$) in control leaves increased rapidly with the increase in PFD (Fig. 3*A*), but in iron-deficient leaves it increased only slightly before PFD reached 600 μmol $m^{-2}$ $s^{-1}$ and then it was at a plateau. These values indicate that only a small part of excitation energy was used in photochemical reaction, but more of it was dissipated in iron-deficient leaves compared to control leaves. In iron-deficient leaves under high irradiance, the dissipated energy was about 60 % of the absorbed radiation. The fraction of photons absorbed in PS2 antenna that was lost *via* thermal energy dissipation (D) of control leaves was much lower than that of iron-deficient leaves (Fig. 3*B*). Also NPQ in iron-deficient leaves was 1.4 times higher than that in control leaves (Fig. 3*C*).

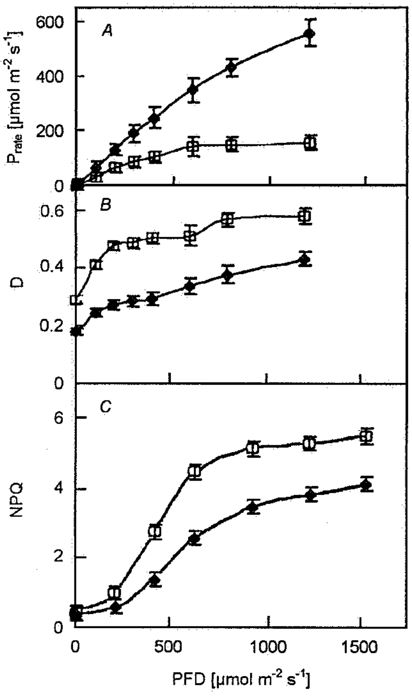

Fig. 3. Changes of photochemical reaction rate, $P_{rate}$ (*A*), fraction of photons absorbed in PS2 antenna that is removed *via* thermal energy dissipation, D (*B*), and nonphotochemical quenching, NPQ (*C*) in control (♦) and iron-deficient (□) maize leaves exposed to different PFD.

**Effect of iron deficiency on energy dissipation depending on xanthophyll cycle and D1 protein turnover**: About 90 % of the total xanthophyll content took the de-epoxidised form (A+Z) in iron-deficient leaves after 3 h of high irradiance, but only about 40 % in control leaves under the same condition (Fig. 4). The NPQ in iron-deficient and control leaves decreased by about 40 and 30 %, respectively, as a result of DTT treatment (Fig. 5*A*). When treated with SM, the NPQ in iron-deficient and control leaves decreased by about 70 and 50 %, respectively (Fig. 5*B*).

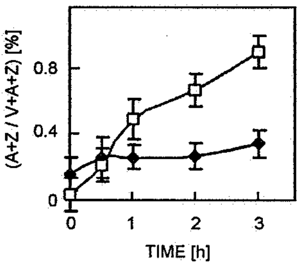

Fig. 4. Changes of de-epoxidation extent of xanthophyll cycle in control and iron deficient maize leaves under high irradiance (1 200 μmol m$^{-2}$ s$^{-1}$).

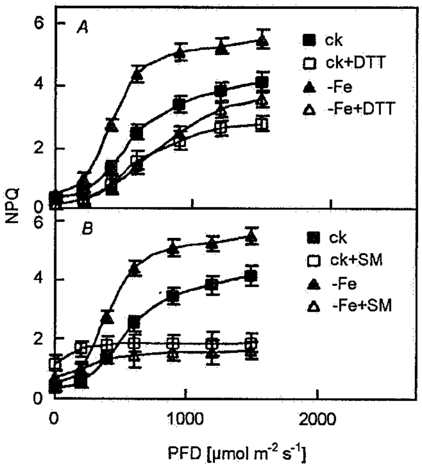

Fig. 5. Changes of nonphotochemical quenching, NPQ in control and iron-deficient leaves treated with dithiothreitol, DTT (*A*) or streptomycin sulphite, SM (*B*) under different irradiance (PFD).

## Discussion

If the decrease in pigment content was the limiting factor for photosynthesis, absorbed radiant energy should increase with increasing PFD in both control and iron-deficient leaves, and thus in both cases $P_N$ should increase with increasing PFD. However, we found only a little increase in $P_N$ due to increase of PFD in iron-deficient leaves (Fig. 1*A*). Hence the decrease in $P_N$ was not caused by the decrease in pigment content. We infer two possible causes of this low $P_N$ despite sufficient PFD and $CO_2$ concentration in iron-deficient maize leaves. One possibility is that the production of NADPH and ATP decreases due to blocked electron transport; the other is a decrease in carbon assimilation. The two photosystems are both iron-containing proteins, but because iron's role in the two systems may be different, the effect of iron deficiency may also be different. We found that the effect of iron deficiency on PS2 was less than that on PS1 and/or carbon assimilation (Fig. 2). To date, there have been no experiments showing that iron is required in the process of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) synthesis and activa-tion. McKey *et al.* (1997) found that serious iron deficiency had little effect on the content of RuBPCO. Therefore, the severe pQ reduction in iron-deficient leaves might be caused by the decrease in electron transport activity of PS1. The dramatically decreased carboxylation efficiency in iron-deficient leaves may be a result of deficiency in NADPH and ATP due to blocked PS1 electron transport. However, it is hard to determine whether and to what extent the activity of RuBPCO is directly affected by iron deficiency. To better understand whether PS1 or carbon assimilation is the limiting factor of photosynthesis in iron-deficient leaves, further direct evidence is needed. Whatever the case may be, iron-deficient leaves would suffer serious acceptor photoinhibition at high irradiance.

Though the amount of absorbed photons declined due to the decrease of Chl content in iron-deficient leaves, the excess photons in iron-deficient leaves might have more serious effect than those observed in control leaves because of blocked electron transport. To avoid photodamage, the excess radiant energy must be dissipated. The fact that about 60 % of excited energy were removed through thermal dissipation at high irradiance indicates that the photosynthetic apparatus can be effectively protected against photodamage in iron-deficient leaves (Fig. 3*B*).

The photochemical reaction rate ($P_{rate}$) in iron-deficient leaves did not stop increasing with increasing irradiance until the PFD reached 600 μmol $m^{-2}$ $s^{-1}$ (Fig. 3*A*). As the saturating irradiance for $P_N$ in iron-deficient leaves was only about 300 μmol $m^{-2}$ $s^{-1}$ (Fig. 1*A*), it is plausible that part of the radiant energy involved in photochemical reaction rate ($P_{rate}$) may not be used in carbon assimilation, but rather to produce active oxygen. Another experiment of ours showed that the production of active oxygen in iron-deficient leaves under high irradiance was 3-4 times as much as under weak irradi-ance (values not shown).

The xanthophyll cycle is an important dissipation mechanism (Björkman 1987, Demmig-Adams 1990, Gilmore 1997, Goss *et al.* 1998), and it may play an important role in iron-deficient leaves. About 90 % deepoxidation was observed in iron-deficient leaves exposed to high irradiance (Fig. 4). When treated with DTT, the decrease of NPQ in iron-deficient leaves was about 1.5 times higher than that in control leaves (Fig. 5*A*). Compared with control, the absolute content of (A+Z) in iron-deficient leaves may be lower, but the ratio of xanthophyll to Chl in iron-deficient leaves was 1.2 times higher than that in control leaves. Higher degree of deepoxidation and higher carotenoid content was clearly a protective response to excess irradiance caused by lower photosynthesis in iron-deficient leaves. However, the xanthophyll cycle may not be the only dissipation mechanism.

Energy dissipation relying on D1 protein turnover is also a very important dissipation mechanism (Sundy *et al.* 1993, Critchley and Russell 1994, Russell *et al.* 1995). When treated with SM, the decrease of NPQ in iron-deficient leaves was about 1.8 times higher than that in control leaves (Fig. 5*B*). Thus energy dissipation depending upon D1 protein turnover was probably very important in iron-deficient leaves. In fact, inactivation of PS2 reaction centres occurred when the synthesis of D1 protein was inhibited, which would lead to decrease of electron transfer and less trans-thylakoid pH gradient build-up. Triggering of the xanthophyll cycle in leaves depends on the formation of trans-thylakoid pH gradient (Briantais *et al.* 1980, Horton *et al.*1994, Gilmore 1997). Hence the xanthophyll cycle may be also partly depressed when SM inhibits the D1 protein synthesis, and there may be a close relationship between xanthophyll cycle and D1 protein turnover.

In iron-deficient leaves the decreased $F_v/F_m$ almost totally recovered during a 30-min dark adaptation after a 3-h exposure to PFD of 1 200 μmol $m^{-2}$ $s^{-1}$, which indicates that photosynthetic apparatus was not damaged in iron-deficient leaves after prolonged high irradiation. Obviously, the photoprotection mechanism depending on xanthophyll cycle and D1 protein turnover was effectively activated in iron-deficient maize leaves. Therefore, we suppose that the xanthophyll cycle and D1 protein turnover are the main photoprotection mechanisms of acceptor photoinhibition occurring in iron-deficient leaves.

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