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Ferredoxin-quinone reductase benefits cyclic electron flow around photosystem 1 in tobacco leaves upon exposure to chilling stress under low irradiance

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Abstract

The function of chloroplast ferredoxin quinone reductase (FQR)-dependent flow was examined by comparing a wild type tobacco and a tobacco transformant (ΔndhB) in which the *ndhB* gene had been disrupted with their antimycin A (AA)-fed leaves upon exposure to chilling temperature (4 °C) under low irradiance (100 µmol m^{-2} s^{-1} photon flux density). During the chilling stress, the maximum photochemical efficiency of photosystem (PS) 2 (F_v/F_m) decreased markedly in both the controls and AA-fed leaves, and $P700^+$ was also lower in AA-fed leaves than in the controls, implying that FQR-dependent cyclic electron flow around PS1 functioned to protect the photosynthetic apparatus from chilling stress under low irradiance. Under such stress, non-photochemical quenching (NPQ), particularly the fast relaxing NPQ component (q_f) and the de-epoxidized ratio of the xanthophyll cycle pigments, (A+Z)/(V+A+Z), formed the difference between AA-fed leaves and controls. The lower NPQ in AA-fed leaves might be related to an inefficient proton gradient across thylakoid membranes (ΔpH) because of inhibiting an FQR-dependent cyclic electron flow around PS1 at chilling temperature under low irradiance.

Additional key words: chlorophyll fluorescence; cyclic electron flow; ferredoxin quinone reductase; *Nicotiana*; non-photochemical quenching; photosystem 2; xanthophyll cycle.

Introduction

The contribution of cyclic electron flow around photosystem (PS) 1 in chloroplast has been a topic of general interest in plant physiology for many years (Heber and Walker 1992, Fork and Herbert 1993, Bendall and Manasse 1995, Shikanai and Endo 2000, Munekage *et al.* 2002, Li *et al.* 2004a). Cyclic electron flow around PS1 functions in adaptation to environment stress (Heber and Walker 1992). First, cyclic electron flow could adjust the productive ratio of NADPH/ATP depending on the requirements of biochemical reactions in the stroma (Mi *et al.* 1992, 1994). Second, the proton gradient generated across the thylakoid membranes prevents severe reduction of the intersystem by means of down-regulating PS2 (Horton *et al.* 1996).

In chloroplast, two pathways sensitive to antimycin A (AA) are recognized as being involved in the cyclic electron flow around PS1. One is the NADH dehydrogenase (NDH)-dependent flow, and the other is the ferredoxin quinone reductase (FQR)-dependent flow (Endo *et al.* 1997, 1998, Munekage *et al.* 2002).

Cyclic electron flow around PS1, which shares a common sequence of electron carriers with linear electron transfers, namely the plastoquinone (PQ) pool, cytochrome b_6/f complex, and plastocyanin (Bendall and Manasse 1995), was first recognized as a FQR activity *in vitro* (Tagawa *et al.* 1963, Mills *et al.* 1979). Although

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Abbreviations: A – antheraxanthin; Chl – chlorophyll; ETR – PS2-driven electron transport rate; F_m – maximal fluorescence with all PS2 reaction centres closed in the dark-adapted state; F_v/F_m – maximal fluorescence efficiency of PS2; F_m' – maximal fluorescence of PS2 in light-adapted state; F_s – steady-state fluorescence in light; F_v – variable fluorescence; F_0 – original fluorescence; FQR – ferredoxin quinone reductase; NDH – NAD(P)H dehydrogenase; NPQ – non-photochemical quenching; P700 – reaction centre chlorophyll of PS1; PFD – photon flux density; PQ – plastoquinone; PS – photosystem; q_f – fast relaxing non-photochemical quenching; q_m – middle relaxing non-photochemical quenching; q_s – slowly relaxing non-photochemical quenching; V – violaxanthin; Z – zeaxanthin.

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FQR possibly catalyzes the main pathway of cyclic electron flow around PS1 rather than NDH in higher plants, the molecular identity of FQR has not been revealed so far (Munekage *et al.* 2002).

Recent research showed that the putative NDH complex containing the *ndhB* gene product mediates the transport of electrons from the stromal electron donors to PQ in cyclic electron flow around PS1 in C_3 plants (Burrows *et al.* 1998, Shikanai *et al.* 1998, Casano *et al.* 2000, Shikanai and Endo 2000). The NDH complex may be involved in cyclic electron flow around PS1 operating *in vivo* in C_3 plants (Shikanai *et al.* 1998, Endo *et al.* 1999, Joët *et al.* 2001, 2002) and the NDH-dependent cyclic electron flow is related to excess energy dissipation (Li *et al.* 2004a).

Plants vary greatly in their ability to survive environmental conditions. In order to adapt to changes of environments, photosynthetic organisms get the delicate balance between efficient light-harvesting under limiting irradiance and regulated dissipation of energy under excess irradiance. Much attention has been focused to NPQ, which can protect the photosynthetic apparatus from inactivation and damage by dissipating excess energy in light-harvesting antenna complexes of PS2 (Horton *et al.* 1994, Xu *et al.* 1999, Li *et al.* 2003, 2004a). The xanthophyll cycle can protect the photosynthetic apparatus from photo-damage under low temperatures (Xu *et al.* 1999, 2000) and its operation depends on the build-up of ΔpH (Demmig-Adams and Adams 1996, Horton *et al.* 1996, Müller *et al.* 2001). The lower NPQ (and also lower de-epoxidized ratio of xanthophyll cycle pigments) in an *ndh*-deficit tobacco mutant (ΔndhB) is related to the build-up of ΔpH (Li *et al.* 2004a). Additionally, the PGR5-dependent pathway is thought to be the main route of the cyclic electron flow around PS1, while the NDH-mediated pathway may play a compensatory function (Munekage *et al.* 2002). In the present work, higher reduction of the stromal NADP pool and of the intersystem electron carriers were induced by inhibiting photosynthesis of tobacco leaves upon exposure to chilling temperature (4 ºC) under low irradiance of 100 μmol m^{-2} s^{-1} PFD (Li *et al.* 2004a). During the stress, excess photon energy, over the possibility of the photosynthetic machinery to utilize, was induced since photosynthesis was inhibited under such conditions (Li *et al.* 2004b). After feeding AA, an inhibitor of both NDH- and FQR-dependent cyclic electron flow around PS1 (Endo *et al.* 1997), the changes of energy dissipation and the de-epoxidized ratio of xanthophyll cycle pigments was obtained in a wild type tobacco and its transformant, in which the chloroplastic *ndhB* gene was insertionally inactivated (ΔndhB), demonstrating that cyclic electron flow around PS1 through the FQR is also related to energy dissipation.

Materials and methods

Plants and chilling treatments: A mutant tobacco with *ndhB*-insertionally inactivated as well as its wild type (*Nicotiana tabacum* cv. Xanthi, see Shikanai *et al.* 1998) was used. Sprouted burgeons were planted into plastic pots (one plant per pot) filled with 5 kg sterilized soil and grown at 25–30/15–20 °C (day/night) under 14/10 h irradiation (300–400 μmol m^{-2} s^{-1})/darkness in the greenhouse. Fully-expanded leaves were harvested from 2- to 3-month-old tobacco plants before treatment. The leaf discs were floated in tap water with the adaxial side face-up in a growth chamber maintained at 4 °C for 6 h. The irradiance provided by fluorescent lamp was 100 μmol m^{-2} s^{-1} PFD at the surface of the leaf discs. Before chilling treatment, leaf discs were acclimated under 100 μmol m^{-2} s^{-1} PFD at 25 °C for about 30 min. Non-chilling controls were treated at 25 °C under 100 μmol m^{-2} s^{-1} PFD.

Chlorophyll (Chl) *a* fluorescence: The maximum photochemical efficiency of PS2 expressed as F_v/F_m was measured with a portable fluorometer (*FMS2*, *Hansatech*, England) according to the protocol described by van Kooten and Snel (1990). NPQ was estimated as NPQ = $(F_m - F_m')/F_m'$, where F_m is the maximum fluorescence measured after dark adaptation (Schreiber *et al.* 1994), F_m' is the maximum yield of fluorescence in light-adapted leaves. PS2-driven electron transport rate (ETR) was calculated as $(1 - F_s/F_m') \times 0.5 \times$ PFD × leaf absorbance (Xu *et al.* 1999), where 0.5 is a factor assuming an equal distribution of absorbed photons between PS2 and PS1, leaf absorbance is taken as 0.85, and F_s is the steady-state fluorescence yield. NPQ can usually be divided into three different components according to their relaxation kinetics in darkness following a period of irradiation (Müller *et al.* 2001). The major and most rapid component of NPQ is the ΔpH- or energy-dependent component q_f. The second component, q_m, relaxes within minutes and is more important in algae, but is rather negligible in most plants during exposure to excess photons. The third component of NPQ, q_s, shows the slowest relaxation and is related to photoinhibition of photosynthesis. q_f is highly correlated with the amount of Z and A synthesized *via* the xanthophyll cycle (Müller *et al.* 2001), and has been measured as described by Quick and Stitt (1989).

820 nm absorbance: Oxidation and reduction of P700 was measured using a *PEA* (Plant Efficiency Analyser) sensor (*Hansatech Instruments*, Kings Lynn, Norfolk, UK) described by Schansker *et al.* (2003). This instrument can measure the transmission change of Chl fluorescence at 820 nm. The first reliable measuring point for fluorescence change was at 20 µs, whereas the first measuring point for transmission change was at 400 µs. The time constant used for the transmission measurements was 100 µs. The irradiance used for the transmission measurements was 3 000 µmol m^{-2} s^{-1} PFD. The radiation was produced by four 650 nm LEDs (light-emitting diodes). The far-red source was a *QDDH73520* LED (*Quantum Devices*, Barneveld, WI, USA) filtered at 720±5 nm. The modulated (33.3 kHz) far-red measuring radiation was provided by an *OD820* LED (*Opto Diode Corp.*, Newbury Park, CA, USA) filtered at 830±20 nm. Executing commands such as turning on and off the LEDs took approximately 250 µs. Turning on the red radiation and starting the measurement were synchronized commands. For the far-red radiation there was a delay of 250 µs between turning on the far-red radiation and the start of the measurement.

Pigment analysis: Leaf discs were immersed in liquid N_2 immediately after F_v/F_m determination and stored at –80 °C until use. Photosynthetic pigments were extracted with 0.5 cm^3 of ice-cold acetone and quantified by reversed-phase high performance liquid chromatography (HPLC) based on a method described by Li *et al.* (2004a).

Feeding inhibitor: AA was used as an inhibitor of NDH- and FQR-dependent cyclic electron flow around PS1 (Endo *et al.* 1997). Leaves were cut at the end of the leaf stalk and placed in vials containing 20 mM AA or water for the control, then the leaves were exposed to 50 µmol(photon) m^{-2} s^{-1} at 25 °C for 4 h.

Results

Photosynthesis of AA-fed leaves is sensitive to chilling stress under low irradiance: During exposure to chilling stress under low irradiance, photoinhibition of PS2 in control and AA-fed leaves was estimated by measuring the maximum photochemical efficiency of PS2 (F_v/F_m) (Fig. 1). Relative to leaves at 25 °C under 100 µmol m^{-2} s^{-1} PFD, F_v/F_m in control and AA-fed leaves decreased during the 6-h chilling stress. The decrease in F_v/F_m was more pronounced in AA-fed leaves than in controls. At the end of chilling stress, F_v/F_m had decreased by about 22.7, 30.7, 32.7, and 46.4 % in wild type control, wild type AA-fed leaves, ΔndhB control, and ΔndhB AA-fed leaves, respectively (Fig. 1*C,D*). Thus the photoinhibitory effect of chilling stress under low irradiance on PS2 was more obvious in AA-fed leaves than in controls. Relative to non-chilling controls, a decrease in initial fluorescence (F_0) was observed in wild type, ΔndhB, and their AA-fed leaves during chilling stress (Fig. 1*A,B*). Similar to F_v/F_m, the ETR decreased rapidly during the first hour of chilling stress and remained constant thereafter in wild type, ΔndhB, and their AA-fed leaves (Fig. 2). ETR in non-chilling controls changed little. During chilling stress under low irradiance, the steady-state level of ETR in AA-fed leaves of both wild type and ΔndhB was slightly lower compared with the related controls (Fig. 2).

Oxidation level of P700 ($P700^+$) decreased in AA-fed leaves under chilling stress: $P700^+$ was measured by the absorbance at 820 nm in both control and AA-fed leaves upon exposure to chilling stress under low irradiance (Fig. 3). At the end of the 6-h chilling stress, $P700^+$ decreased by about 19.7, 31.8, 24.7, and 34.7 % in wild type control, wild type AA-fed leaves, ΔndhB control, and ΔndhB AA-fed leaves, respectively (Fig. 3*A.B*). It seems that 6-h chilling stress affected the redox state of P700.

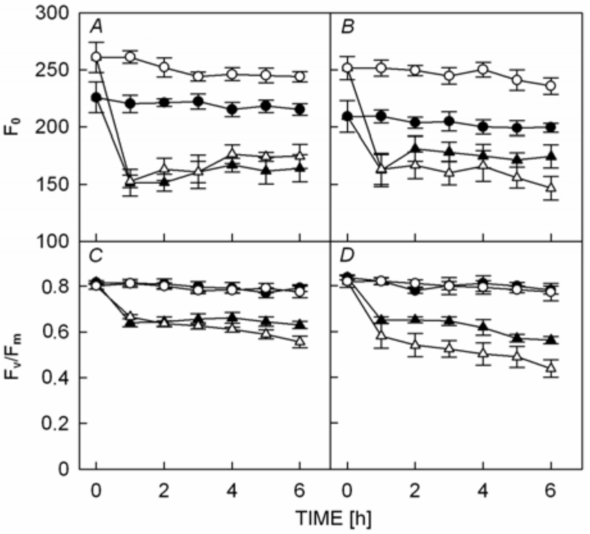

Fig. 1. Effects of antimycin A (AA) on the initial fluorescence (F_0) and the maximum photochemical efficiency of photosystem 2 (F_v/F_m) in tobacco leaves. Control (*closed symbols*) and AA-fed (*open symbols*) leaf discs of wild type (*A,C*) and ΔndhB (*B,D*) were exposed to 100 µmol(photon) m^{-2} s^{-1} at 4 °C (*triangles*) and 100 µmol(photon) m^{-2} s^{-1} at 25 °C (*circles*), respectively. Chlorophyll fluorescence was measured after 5-min dark adaptation. Means ± SD of 5 measurements on separate leaves.

NPQ induction is partially reduced in AA-fed leaves under chilling stress: The dissipation of excess photon energy as heat was monitored by measuring the development of NPQ during the 6-h chilling stress (Fig. 4*A,B*). Relative to non-chilling controls, NPQ increased when these plants were exposed to chilling stress under low irradiance. NPQ in AA-fed leaves was lower than that in controls during chilling stress.

To estimate the major and fast component (q_f) of NPQ, the dark relaxation kinetics at 25 ºC after various

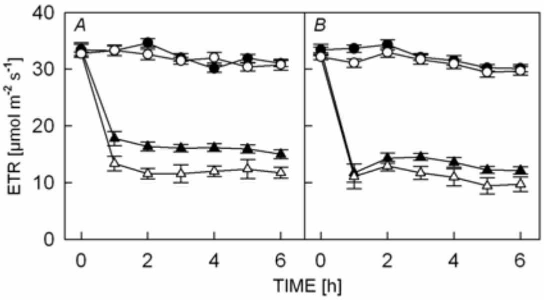

Fig. 2. Effects of antimycin A (AA) on the PS2-driven electron transport rate (ETR) *in vivo* in tobacco leaves. Control (*closed symbols*) and AA-fed (*open symbols*) leaf discs of wild type (*A*) and ΔndhB (*B*) were exposed to 100 μmol(photon) m^{-2} s^{-1} at 4 °C (*triangles*) and 100 μmol(photon) m^{-2} s^{-1} at 25 °C (*circles*), respectively. Chlorophyll fluorescence was measured after 5-min dark adaptation. Means ± SD of 5 measurements on separate leaves.

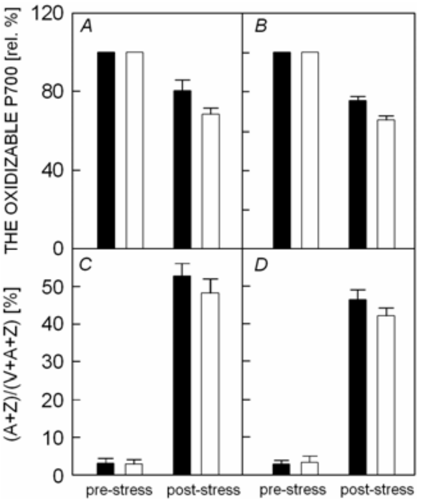

Fig. 3. Effects of antimycin A (AA) on the oxidizable P700 (*A,B*) and the xanthophyll cycle conversion (*C,D*) in tobacco leaves. Control (*closed bars*) and AA-fed (*open bars*) leaf discs of wild type (*A,C*) and ΔndhB (*B,D*) were exposed to 100 μmol(photon) m^{-2} s^{-1} at 4 °C and 100 μmol(photon) m^{-2} s^{-1} at 25 °C, respectively. Chlorophyll fluorescence was measured after 5 min dark adaptation. Means ± SD of 5 measurements on separate leaves.

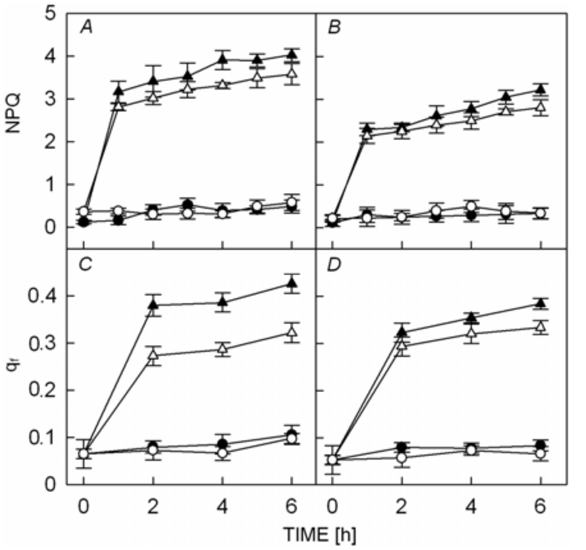

Fig. 4. Effects of antimycin A (AA) on non-photochemical quenching (NPQ) and its fast component, q_f, in tobacco leaves. Control (*closed symbols*) and AA-fed (*open symbols*) leaf discs of wild type (*A,C*) and ΔndhB (*B,D*) were exposed to 100 μmol(photon) m^{-2} s^{-1} at 4 °C (*triangles*) and 100 μmol(photon) m^{-2} s^{-1} at 25 °C (*circles*), respectively. Chlorophyll fluorescence was measured after 5 min dark adaptation. Means ± SD of 5 measurements on separate leaves.

periods of irradiation at 4 ºC were analyzed (Fig. 4*C,D*). The kinetics of q_f in both control and AA-fed leaves increased rapidly during chilling stress. This is consistent with the changes of NPQ during chilling stress (Fig. 4*A,B*). During the whole period of stress, the values of q_f were lower in AA-fed leaves than in controls.

Zeaxanthin (Z) and antheraxanthin (A) accumulated in both control and AA-fed leaves at the end of the chilling stress period (Fig. 3*C,D*). At the end of 6-h stress, the de-epoxidized ratio of the xanthophyll cycle pigments, (A+Z)/(V+A+Z), was smaller in AA-fed leaves than in controls. The accumulation of Z+A was consistent with the values of NPQ and q_f in both controls and AA-fed leaves at the end of the stress period (Fig. 4).

Discussion

The direction of F_0 change depends on the dominant factor between the energy dissipation and the inactivation or damage of PS2 (Xu and Wu 1996). An increase in NPQ leads to a decrease in F_0 (Ögren and Öquist 1984) and the inactivation or the damage of PS2 causes the increase of F_0 (Xu and Wu 1996). We found that chilling stress did not damage PS2 reaction centres of wild type, ΔndhB, and their AA-fed leaves since F_0 decreased during chilling stress (Fig. 1*A,B*). The NDH-dependent cyclic electron flow around PS1 has been proposed to protect PS1 and PS2 by comparing ΔndhB, in which the *ndh*B gene had been disrupted, with its wild type at chilling temperature under low irradiance (Li *et al.* 2004a). This showed substantial differences in sensitivity to chilling-induced photoinhibition between wild type and ΔndhB controls and their AA-fed leaves as indicated by the decrease in F_v/F_m (Fig. 1*C,D*) and $P700^+$ (Fig. 3*A,B*). Inhibiting FQR-dependent cyclic electron flow around PS1 by AA (Endo *et al.* 1997), both wild type and ΔndhB were more sensitive to chilling stress under low irradiance. The similar effects of AA on both wild type and ΔndhB during stress are attributed to the loss of cyclic electron flow around PS1, including NDH-dependent and FQR-dependent pathways, since both these two pathways can be inhibited by AA (Endo *et al.* 1997).

Chilling stress under low irradiance could cause an accumulation of reducing power on the acceptor side of PS1 (Terashima *et al.* 1994, Sonoike 1996, Li *et al.* 2003, 2004a). It is obvious that the limited electron acceptors caused the decrease of $P700^+$ in both controls and their AA-fed leaves (Fig. 3*A,B*) when the Calvin cycle was inhibited at chilling temperature under low irradiance (Li *et al.* 2004b), thus electrons accumulated in the carrier at the PS1 acceptor side. Hence, if the Fe-S centres' F_X, F_A, and F_B are reduced, recombination in the radical pairs $P700^+A_0^-$ and/or $P700^+A_1^-$ can occur when the Fe-S centres are not oxidized by an external acceptor within the time of the back-reaction (Barth *et al.* 2001). In AA-fed leaves, FQR inhibition causes a more severe reduction state of the stroma (Fig. 3*A,B*).

Cyclic electron flow is essential to dissipate photon energy preventing thus stromal components from over-reduction (Endo *et al.* 1999). From the difference of F_v/F_m (Fig. 1*C,D*), ETR (Fig. 2), and $P700^+$ (Fig. 3*A,B*) between controls and AA-fed leaves at chilling temperature under low irradiance, it can be speculated that the FQR-dependent cyclic electron flow around PS1 could operate at 4 °C under low irradiance of 100 μmol m^{-2} s^{-1} PFD and could protect photosystems from more severe photoinhibition. The decrease in ETR (Fig. 2) was accompanied by the increase in NPQ (Fig. 4*A,B*) and q_f (Fig. 4*C,D*). This indicates that it can cause the accumulation of assimilation power and protons in the thylakoid lumen, as shown by the increase in q_f (Fig. 4*C,D*) when the Calvin cycle was inhibited at chilling temperature under low irradiance (Li *et al.* 2004b). The decrease of ETR in AA-fed leaves of ΔndhB (Fig. 2*B*) during chilling stress under low irradiance also implied that the FQR-dependent pathway might exist in tobacco leaves besides the NDH-dependent pathway. It seems that the substantial difference between control and AA-fed leaves was observed only at chilling temperature under low irradiance (Figs. 1 and 2), but not at 25 °C. Tobacco is in a good physiological state at 25 °C (Figs. 1 and 3), and 100 μmol m^{-2} s^{-1} PFD is a low level to be utilized, thus, inhibiting cyclic electron flow around PS1 by AA can not affect its physiological state obviously under non-chilling conditions.

A close relationship between the development of NPQ and the accumulation of Z and A has often been reported (Demmig-Adams and Adams 1996, Xu *et al.* 1999, Li *et al.* 2003, 2004a). Z and possibly A formed *via* the xanthophyll cycle are involved in q_f induction (Demmig-Adams and Adams 1996). Such a relationship could also be reflected by the levels of q_f and (Z+A)/(V+Z+A) in control and AA-fed leaves of tobacco (Figs. 3*C,D* and 4*C,D*). Cyclic electron flow around PS1 could generate a proton gradient across thylakoid membranes (ΔpH), which is related to NPQ, especially under limiting conditions of the electron acceptor from PS1 (Shikanai and Endo 2000, Li *et al.* 2004a). The higher q_f (Fig. 4*C,D*) and higher de-epoxidized ratio of the xanthophyll cycle (Fig. 3*C,D*) in the controls show that FQR-dependent cyclic electron flow around PS1 is also beneficial for the build-up of an extra proton gradient across the thylakoid membranes, which contributes to the xanthophyll cycle-dependent energy dissipation (Demmig-Adams and Adams 1996, Horton *et al.* 1996, Müller *et al.* 2001). In addition, reduced NPQ in AA-fed leaves might have little effect on the over-reduction of the stroma since PS1 photoinhibition has no relation to the xanthophyll cycle in AA-fed leaves, which lack the ability of drastic NPQ induction at chilling temperature (Havaux and Kloppstech 2001). Thus, besides the inhibition of carbon metabolism at low temperature (Li *et al.* 2004b), the inhibition of an FQR-dependent cyclic electron flow caused the more severe reduction state of the stroma in AA-fed leaves (Fig. 3*A,B*).

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