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Down-regulation of photosystem 2 efficiency and spectral reflectance in mango leaves under very low irradiance and varied chilling treatments

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Abstract

In order to elucidate the effects of chilling-stress at night on photosystem 2 (PS2) efficiency under dim irradiance (DI), mango leaves were chilled to varied extent (8–3 °C) and for varied duration (0–12 h) in growth cabinets in the dark, and then exposed to DI (20 µmol m^{-2} s^{-1} PPFD) at each chilling-temperature for 1 h. Chilling in the dark had little effect on F_v/F_m of mango leaves. But both the extent and duration of chilling pre-treatments significantly affected F_v'/F_m' when leaves were exposed to DI. This down-regulation of PS2 efficiency was closely related to xanthophyll de-epoxidation, assessed as photochemical reflectance index (PRI) and calculated from leaf spectral reflectance $[(R_{531} - R_{570})/(R_{531} + R_{570})]$, and non-photochemical quenching (NPQ). The down-regulation of PS2 is a defence mechanism initiated at predawn in winter to alleviate the damage of PS2 by the sudden and strong irradiation at sunrise. Mango leaves, transferred suddenly from warm and dark room to DI and chilling showed a slight down-regulation of PS2 efficiency, in spite of an increased xanthophyll de-epoxidation. This might have been due to the unavailability of some cofactors required for NPQ.

Additional key words: chlorophyll fluorescence; dim irradiance; leaf spectral reflectance; low temperature; *Mangifera indica*.

Introduction

The efficiency of photosystem 2 (PS2) of plants is influenced by environmental factors. In habitats fully exposed to sun, leaves may absorb more photons than that they can utilize, and this excessively absorbed energy often leads to a reduced efficiency of PS2 (Demmig-Adams and Adams 1992, Long *et al.* 1994, Osmond and Grace 1995). Plants utilize several mechanisms, including xanthophyll cycle, to alleviate the damage caused by absorbing excess photon energy. In xanthophyll cycle, a carotenoid pigment violaxanthin is de-epoxidized into antheraxanthin and zeaxanthin; and zeaxanthin binds with proteins to effect non-photochemical quenching (NPQ) (Li *et al.* 2000, Morosinotto *et al.* 2001, Holt *et al.* 2005).

Gamon *et al.* (1990, 1993) demonstrated that the inter-conversion of xanthophyll cycle pigments could be detected in intact leaves as subtle changes in reflectance at 531 nm. Photochemical reflectance index $[PRI = (R_{531} - R_{570})/(R_{531} + R_{570})]$, a reflectance-based photosynthetic index defined by Gamon *et al.* (1992), correlates with the epoxidation state of xanthophyll cycle pigments and photosystem efficiency in many studies with diverse conditions, such as under varied irradiance (Peñuelas *et al.* 1994, Gamon *et al.* 1997, 2001, Gamon and Surfus 1999, Guo and Trotter 2004), different nitrogen levels (Gamon *et al.* 1992, Peñuelas *et al.* 1994), and seasons (Stylinski *et al.* 2002), as well as in different species (Gamon *et al.* 1997, Stylinski *et al.* 2002, Guo and Trotter 2004). Leaf spectral reflectance allows an easy, rapid, and instantaneous assessment of contents of xanthophyll cycle pigments. While traditional and destructive measurements, such as HPLC, require changing leaf samples throughout the measuring course, non-intrusive fluorescence or reflectance measurements require fewer leaf samples and can reduce experimental errors by monitoring one leaf sample throughout a time course for different treatments or conditions.

Under some environmental stresses, such as low temperature, excessively absorbed photons could increase the stress-induced decline in photosynthetic capacity because reactions of Calvin cycle are affected to a greater

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Abbreviations: Chl – chlorophyll; DI – dim irradiance; F_v/F_m – potential efficiency of PS2; F_v'/F_m' – actual efficiency of PS2 under irradiation; HI – high irradiance; NPQ – non-photochemical quenching; PPFD – photon flux density; PRI – photochemical reflectance index $[(R_{531} - R_{570})/(R_{531} + R_{570})]$; PS2 – photosystem 2.

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extent than the processes of photon absorption and election transport (Baker 1994, Leegood 1995). High irradiance (HI) at low temperature significantly down-regulates PS2 efficiency and increases xanthophyll de-epoxidation (Verhoeven *et al.* 1998, Adams *et al.* 2001, Tsonev *et al.* 2003). Furthermore, chilling in the dark (night) could subsequently reduce the photosynthetic characteristics of plants in daytime (Szalai *et al.* 1996, Allen *et al.* 2000, Ying *et al.* 2002, Guo and Cao 2004), and the decline was associated with the extent and duration of low temperature exposure (Szalai *et al.* 1996, Ying *et al.* 2002, Guo and Cao 2004).

Mango, a tropical-origin fruit tree, has been increasingly cultured in temperate regions, such as the USA, Western Europe, and Japan, during the last decade (Allen *et al.* 2000). Warm-climate plants, with their photosynthesis substantially reduced after chilling (Szalai *et al.* 1996, Allen and Ort 2001), could rapidly down-regulate their PS2 efficiency (Li *et al.* 2004, Watson *et al.* 2004) as well as enhance their xanthophyll de-epoxidation (Watson *et al.* 2004, Xu *et al.* 2004) under chilling temperature and low irradiance (100–250 µmol m^{-2} s^{-1} of photosynthetic photon flux density, PPFD) within one day. In subtropical regions, chilling temperatures (*i.e.* <10 °C) coincide frequently with bright mornings (*i.e.* HI) as a result of rapid heat dissipation by emission of long-wave radiation in clear night. For chilling-sensitive plants grown in subtropical and temperate regions, it is important to elucidate the effect of chilling stress in winter night to PS2 efficiency in the morning under the chilling temperatures and HI. However, most studies on dark-chilling effects, including those on mango, measured photosynthetic characteristics at HI and warm temperatures (Allen *et al.* 2000, Lidon *et al.* 2001, Ying *et al.* 2002). We found that mango could down-regulate its PS2 efficiency under chilling temperatures and very low irradiance (DI), *i.e.* 20 µmol m^{-2} s^{-1} PPFD. Thus, it may be regarded as a defence mechanism initiated at predawn in the winter to alleviate the potential damage of PS2 by the sudden and strong irradiance at sunrise.

In this study, detached mango leaves were chilled in growth cabinets at different temperatures and dim irradiance (DI), and their PS2 efficiency and the inter-conversion of xanthophyll cycle pigments were measured, respectively, by monitoring the chlorophyll (Chl) fluorescence and leaf spectral reflectance.

Materials and methods

Experiments were carried out in February and March 2005 at the National Chung-Hsing University, Taichung, Taiwan (24°10'N, 78 m). The averaged minimum daily temperatures within 1-week prior to measurements in February and March were *ca.* 12 and 15 °C, respectively. South-facing and fully sun-exposed leaves detached from mango (*Mangifera indica* L. cv. Aiwen) were used as the experimental materials. Schedules of chilling-treatments, irradiance, and the time course of measurements are shown in Fig. 1. First, the mango leaves were acclimated in a dark room (room temperature *ca.* 18–20 °C). Then they were put in growth cabinets at 8, 5, and 3 °C for 12, 4, 2, and 0 h at each temperature in the dark. Subsequently, the leaves were irradiated with 20 µmol m^{-2} s^{-1} PPFD for 1 h by fluorescent lamp in the same growth cabinet and temperature as dark-chilling treatment. The efficiency of PS2 was estimated from the ratio between photon-induced variable and maximum fluorescence of dark-adapted (F_v/F_m), or DI (20 µmol m^{-2} s^{-1} PPFD) exposed (F_v'/F_m') leaves, and xanthophyll de-epoxidation was estimated from PRI, calculated from leaf spectral reflectance $[(R_{531} - R_{570})/(R_{531} + R_{570})]$.

Chl fluorescence and leaf spectral reflectance were measured (*a*) before dark-chilling, (*b*) at the end of dark-chilling, (*c*) at the end of light-chilling, (*d*) 20 min after transfer to the dark in each chilling-temperature, and (*e*) 1 h and (*f*) 2 h after transfer to 12 °C in the dark. While (*c*) was measured under DI, the other variants were measured in the dark. Measurements were made under room temperature (*ca.* 18–20 °C) for (*a*), at each chilling temperature (8, 5, or 3 °C) for *b*, *c*, and *d*, and at 12 °C for *e* and *f*.

Chl fluorescence parameters (F_v/F_m, F_v'/F_m', and NPQ) were obtained from a portable pulse amplitude modulated fluorometer (*PAM-2000*, *Walz*, Effeltrich, Germany). The maximum and intrinsic quantum efficiency of PS2 (F_v/F_m and F_v'/F_m') were calculated from $(F_m - F_0)/F_m$ and $(F_m' - F_0')/F_m'$, respectively; and radiation dissipated through non-photochemical quenching (NPQ) was calculated from $F_m/F_m' - 1$ (Bilger and Björkman 1990, Demmig-Adams *et al.* 1996, Adams *et al.* 1999, Allen and Ort 2001, Bachmann *et al.* 2004). F_m and F_m' are the maximal fluorescence, and F_0 and F_0' are the minimal fluorescence in dark-adapted (20 min or more) and irradiated (measured after far-red irradiation)

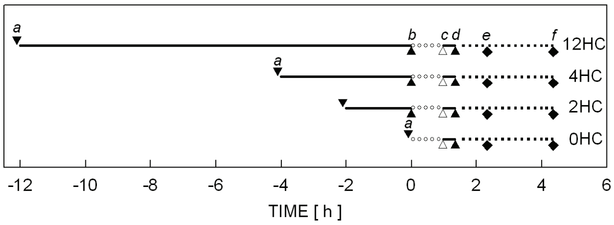

Fig. 1. Schedule of chilling-treatments, irradiance, and time course of measurements. *Solid line*: chilling (8, 5, and 3 °C) in the dark. *Empty dotted line*: treatment with 20 µmol m^{-2} s^{-1} PPFD at each chilling-temperature. *Solid dotted line*: recovery at 12 °C in the dark. *a*, measured at room temperature (*ca.* 18–20 °C) after dark-adaptation for at least 20 min; *b* and *d*, measured at each chilling-temperature in the dark; *c*, measured under 20 µmol m^{-2} s^{-1} PPFD at each chilling-temperature; *e* and *f*, measured at 12 °C in the dark. HC means h of dark-chilling

leaves, respectively. Leaf spectral reflectance was recorded with an interval of 0.3–0.4 nm by a portable narrow-band width spectra-radiometer (*CI-700*, *CID*, USA), a leaf probe (*CI-700*, *CID*, USA), and a tungsten-halogen light source (*CID*, USA, 350–2 000 nm). A white standard panel (*Spectrlon*, *CI-700WR*, *Labsphere*, USA) was used to calibrate the radiometer. Three leaves were sampled from 3 plants, and each leaf was measured 6–8 times. The average of each leaf was used as statistical parameter of each replication.

Results

During the winter, more excess energy is absorbed due to the low temperature and may cause inhibition of enzymatic steps of photosynthesis in plants (Baker 1994, Leegood 1995). Therefore, the recovery of PS2 efficiency becomes slow in winter, and plants often retain large amounts of xanthophyll cycle pigments antheraxanthin and zeaxanthin, and exhibit sustained low PS2 efficiency (Verhoeven *et al.* 1996, 1998, Close *et al.* 2001). Since both F_v/F_m and PRI before treatment varied with the temperature of each measuring day ($F_v/F_m = 0.61–0.74$ and 0.76–0.80, PRI = –0.057 – –0.117 and –0.038 – –0.077 in February and March, respectively), relative values of F_v/F_m, F_v'/F_m', as well as PRI were used in the present study in order to compare the effects of DI and temperatures on Chl fluorescence and PRI in different seasons.

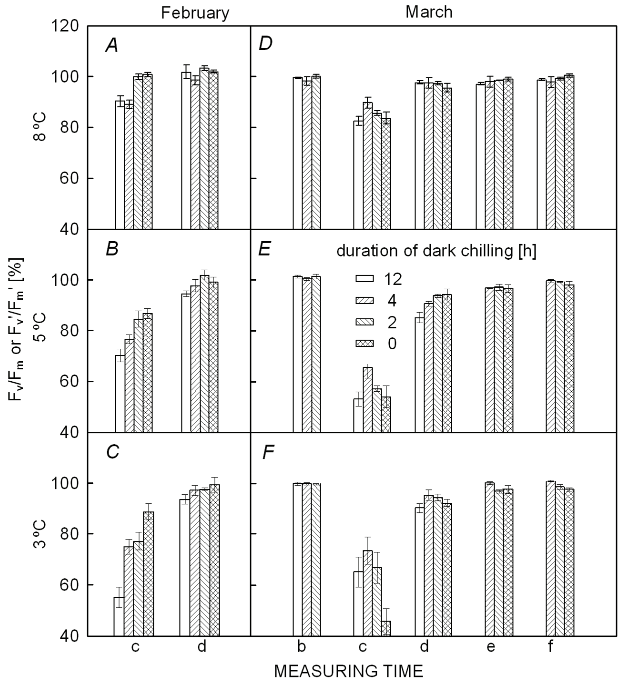

Fig. 2. Effects of dark chilling and dim irradiance on the efficiency of energy conversion of PS2 (F_v/F_m and F_v'/F_m', F_v/F_m before treatment as 100 %), and its reversion at 12 °C in the dark. Measuring times are shown in Fig. 1. $n = 3$; *error bars* are SE.

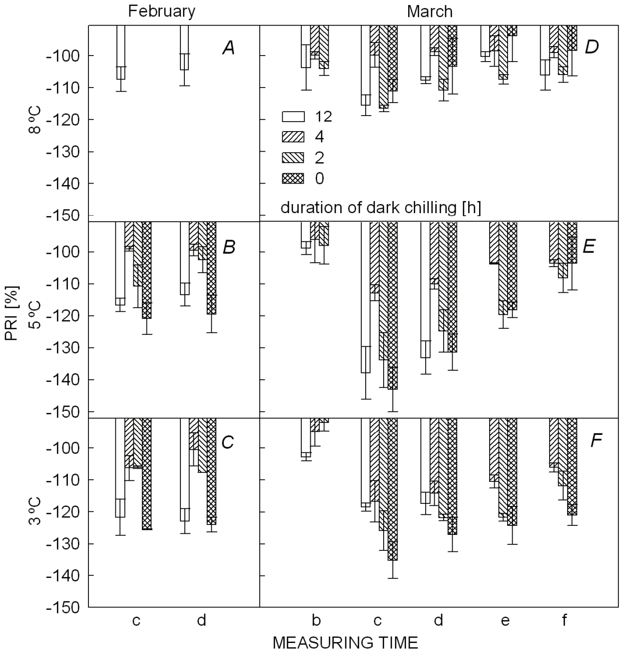

Fig. 3. Effects of chilling and dim irradiance on xanthophyll de-epoxidation [estimated from photochemical reflectance index, PRI, calculated from leaf spectral reflectance, $= (R_{531} - R_{570})/(R_{531} + R_{570})$, before treatment as –100 %], and its reversion at 12 °C in the dark. Measuring times are shown in Fig. 1. $n = 3$; *error bars* are SE.

Effects of dark-chilling and DI on the efficiency of energy conversion of PS2, and its reversion in the dark are shown in Fig. 2. All chilling-treatments in the dark did not affect the maximum efficiency of PS2 (assessed as F_v/F_m) of mango leaves before they were exposed to DI (Fig. 2*D–F*). But most treatments exhibited pronounced decrease in energy conversion efficiency of open PS2 reaction centres (F_v'/F_m'), when mango leaves were subsequently exposed to 20 μmol m^{-2} s^{-1} PPFD for 1 h at each chilling temperature (Fig. 2*A–F*). The decreasing rates of F_v'/F_m' (F_v/F_m before treatment as 100 %) in February and March varied with the duration of dark-chilling (12, 4, 2, and 0 h) and the degree of chilling (3, 5, or 8 °C). In February, F_v'/F_m' was not be affected by DI at 8 °C when mango leaves were pre-treated with 0 and 2 h of dark-chilling (0HC and 2HC), while F_v'/F_m' decreased to *ca.* 90 % when they were pre-treated with 4 and 12 h of dark-chilling (4HC and 12HC) (Fig. 2*A*). On the contrary, at 3 and 5 °C, F_v'/F_m' of 0HC and 2HC decreased to *ca.* 80–90 %, and that of 4HC and 12HC decreased to *ca.* 55–70 %, respectively (Fig. 2*B–C*). Hence F_v'/F_m' declined to a lesser extent at higher temperature and shorter dark-chilling duration, and more drastically at lower temperature and longer chilling duration. On the contrary, in March F_v'/F_m' of all treatments decreased to 90–46 %, more drastically than in February at the same chilling-temperature (Fig. 2*D–F*). In addition, the decline pattern of F_v'/F_m' at each chilling-temperature was different from that obtained in February. 0HC and 12HC showed the largest decline, followed by 2HC, with 4HC showing the slightest decline of F_v'/F_m' (Fig. 2*D–F*).

Similar patterns of PRI variation (being negative in the present study, PRI value of each leaf before treatment is taken as –100 %) could be found in both February and March under chilling and DI treatments (Fig. 3). This PRI variation pattern was parallel to that of F_v'/F_m' obtained in March (Fig. 2*D–F*). However, results obtained in February indicate that the variation of PRI for 0HC and 2HC treatments, particularly 0HC, was opposite to the variation of F_v'/F_m'. Therefore, a significant correlation between relative F_v'/F_m' (F_v/F_m before treatment as 100 %) and relative PRI (PRI before treatment as –100 %) could be found by merging all data obtained in February and March, yet, excluding the data from 0HC treatments in February (Fig. 4*A*). F_v'/F_m' was also closely related to NPQ, pooling data from all chilling-treatments from two months (Fig. 4*B*). NPQ was also closely related to the relative PRI (Fig. 5) when data from 0HC treatments in February were excluded.

Mango leaves exposed to DI and then transferred to the dark regained rapidly their energy conversion efficiency, F_v/F_m (Fig. 2*D–F*). While F_v/F_m of 12HC recovered completely within 80 min (20 min at each chilling temperature + 60 min at 12 °C), full recovery of F_v/F_m of leaves of the remaining treatments was observed within 20 min at each chilling temperature. On the contrary, the recovery of PRI in the dark was slower than that of F_v/F_m. For chilling treatments at 8 and 5 °C, it required *ca.* 80 min (20 min at 8 °C + 60 min at 12 °C) and 140 min (20 min at 5 °C + 120 min at 12 °C), respectively, for the recovery to become near completion. But the recovery of PRI for chilling treatments at 3 °C was still incomplete after 140 min (Fig. 3*D–F*).

Discussion

Our results indicate that chilling in the dark prior to exposing mango leaves to DI had little effect on F_v/F_m (Fig. 2*D–F*). However, we found that under chilling temperatures mango leaves could down-regulate their PS2 efficiency at irradiance (20 µmol m^{-2} s^{-1} PPFD) much lower than that for other species (100–250 µmol m^{-2} s^{-1} PPFD) (Szalai *et al.* 1996, Li *et al.* 2004, Watson *et al.* 2004).

In view of the significant correlation between F_v'/F_m' and NPQ observed by merging data of all treatments in February and March (Fig. 4*B*), we propose that the down-regulation in PS2 efficiency of mango leaves was closely related to the thermal energy dissipation in antennae (Allen and Ort 2001, Adams *et al.* 2004). Parallel changes in PRI and xanthophyll cycle pigment contents have been noted in many studies (Gamon *et al.* 1992, 1997, 2001, Peñuelas *et al.* 1994, Gamon and Surfus 1999, Stylinski *et al.* 2002). The relationship between NPQ and PRI obtained in this study (Fig. 5) renders the conclusion that the down-regulation of PS2 efficiency in mango leaves under DI at chilling-temperatures was closely related to the xanthophyll cycle-dependent energy dissipation.

In many cases, a complete recovery of the reduction in PS2 efficiency within 30 min to several hours represents a reversible metabolic adjustment to changing conditions and may be considered as an acclimatory down-regulation with an indispensable photo-protective role in leaves (Allen and Ort 2001, Müller *et al.* 2001, Adams *et al.* 2004). The current results suggest that mango leaves exposed to DI could rapidly regain their photon energy conversion efficiency when allowed to recover in the dark, and the recovery was complete within 20 min at each chilling temperature for most

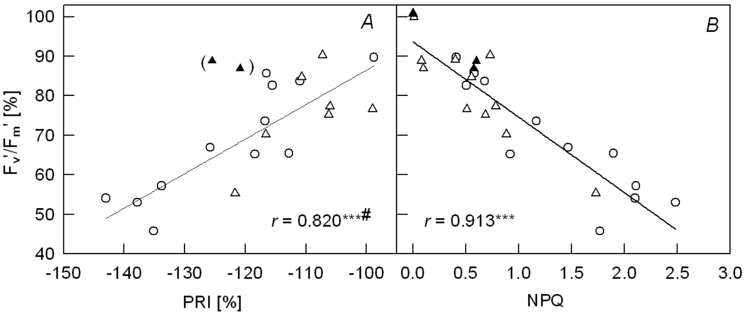

Fig. 4. Relationships between efficiency of energy conversion of PS2 (F_v'/F_m', F_v/F_m before treatment as 100 %) and relative PRI [photochemical reflectance index, calculated from leaf spectral reflectance, = $(R_{531} - R_{570})/(R_{531} + R_{570})$, before treatment as –100 %], and non-photochemical quenching (NPQ) for all chilling-treatments in February (□ and ▲) and March (○) when mango leaves were exposed to dim irradiance at each chilling temperature. $^{***}p<0.001$; $^{\#}$excluding data of leaves without dark-chilling pre-treatment in February (▲).

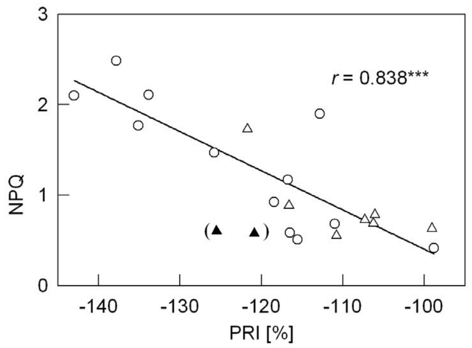

Fig. 5. Relationships between non-photochemical quenching (NPQ) and relative PRI [photochemical reflectance index, calculated from leaf spectral reflectance, == $(R_{531} - R_{570})/(R_{531} + R_{570})$, before treatment as –100 %] for all chilling-treatments in February (□ and ▲) and March (○) when mango leaves were exposed to dim irradiance at each chilling temperatures for 1 h. $^{***}p<0.001$; $^{\#}$excluding data of leaves without dark-chilling pre-treatment in February (▲).

treatments (Fig, 2). Therefore, this down-regulation could be considered as a photo-protective measure (Allen and Ort 2001, Müller *et al.* 2001, Adams *et al.* 2004), and not due to the damage of photosystem (Szalai *et al.* 1996). The down-regulation of PS2 efficiency and simultaneous enhancement of xanthophyll de-epoxidation under DI, *i.e.* 20 μmol m^{-2} s^{-1} PPFD, could be regarded as a mechanism initiated at predawn in the winter to alleviate the potential damage of PS2 by the sudden and strong irradiation at sunrise. Allen *et al.* (2000) reported that overnight chilling of mango leaves did not influence their F_v/F_m the following day, an observation that might be explained by the protection mechanism for PS2 described above.

Figs. 2*D–F* and 3*D–F* indicate that after exposure of mango leaves to DI under chilling-temperatures, the recovery of PRI in the dark was slower than that of F_v/F_m. A slow recovery for xanthophyll de-epoxidation was found in shade leaves of *Euonymus kiautschovicus* (Verhoeven *et al.* 1998) and sun leaves of *Malva neglecta* (Verhoeven *et al.* 1996), when they were transferred from subfreezing temperatures in the field to room temperature. It was also found in Virginia creeper leaves from both shaded and open sites when they were subjected to HI and then allowed to recover under low irradiance (Bachmann *et al.* 2004). Adams *et al.* (1999) pointed out that in the understory, PS2 efficiency of two vines changed rapidly in response to the incident irradiance whereas the xanthophyll cycle began its de-epoxidization following the first major sunfleck in the morning and remained largely de-epoxidized throughout the day, even during periods when the leaves received only diffuse radiation of low irradiance. Thus, leaves in the understory could be rapidly engaged in energy dissipation while exposed to sunflecks. Perhaps, a slow recovery for xanthophyll de-epoxidation might be another mechanism for preventing the damage of PS2 caused by a sudden exposure to strong sunlight.

Chilling in the night results in a decline of the photosynthesis characteristics when leaves are irradiated the next day (Allen *et al.* 2000, Ying *et al.* 2002, Guo and Cao 2004), and this decline is associated with the extent and duration of dark-chilling (Ying *et al.* 2002). Our results indicate that in February the decline of F_v'/F_m' was slight at higher temperature and shorter dark-chilling duration. However, in March F_v'/F_m' showed more drastic decline for mango leaves pre-treated with both nil (0HC) and long (12HC) dark-chilling, while leaves receiving 4 h dark-chilling showed the slightest decline of F_v'/F_m' (Fig. 2). The decline of PRI in February and March showed the same tendency as the decline of F_v'/F_m' in March (Fig. 3). These results indicate that at 0HC treatment in February, in spite of an increased xanthophyll de-epoxidation (lower PRI, Fig. 3*A–C*), mango leaves still showed lower down-regulation of PS2 efficiency (higher F_v'/F_m', Fig. 2*A–C*) and lower NPQ (Fig. 4). The same tendency was found in some antennae-protein deficit mutants, such as an *Arabidopsis* mutant *npq4*, capable of zeaxanthin synthesis but lacking PsbS protein, and thus showing low NPQ in high irradiance (Li *et al.* 2000, Külheim *et al.* 2002). These results indicate that xanthophylls are necessary, but insufficient for energy dissipation by thermal processes; perhaps some proteins are required to bind zeaxanthin to form a complex which could induce a significant quenching effect (Li *et al.* 2000, Morosinotto *et al.* 2003, Ensminger *et al.* 2004, Holt *et al.* 2005). The absence of a parallel changing between NPQ and PRI in leaves was probably due to the unavailability of some cofactors, such as proteins, required for non-photochemical quenching, when these leaves were suddenly exposed to chilling-temperature and DI without dark-chilling pre-treatment. With temperature in February being generally lower than in March, plants should have a higher ability to dissipate the excess energy. Then, why was the non-photochemical quenching of 0HC leaves in February lower than that in March? Hikosaka *et al.* (2004) reported that increased inactivation of PS2 (a decrease of F_v/F_m) could reduce the energy partitioned to PS2. In the present study, F_v/F_m before treatment in February (*i.e.* 0.61–0.74) was lower than that in March (0.76–0.80), suggesting a more inactive PS2 in February probably led to a decreased energy partition to active PS2.

In this work, we used two non-intrusive measurements to estimate the PS2 efficiency and inter-conversion of xanthophyll cycle pigments of chilling-stressed mango leaves. We found that mango leaves could down-regulate their PS2 efficiency at irradiance much lower than that reported for other species. This down-regulation was closely related to the xanthophyll cycle-dependent energy dissipation in the antennae. But, no parallel changing between PS2 efficiency and inter-conversion of xanthophyll cycle pigments could be found when the leaves were suddenly exposed to chilling-temperature and DI without dark-chilling pre-treatment, and this was probably due to the unavailability of some cofactors, such as proteins, required for non-photochemical quenching.

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