

## Estimating heat tolerance among plant species by two chlorophyll fluorescence parameters

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### Abstract

The heat tolerance of 8 temperate- and 1 subtropical-origin  $C_3$  species as well as 17 tropical-origin ones, including  $C_3$ ,  $C_4$ , and CAM species, was estimated using both  $F_0$ -T curve and the ratio of chlorophyll fluorescence parameters, prior to and after high temperature treatment. When leaves were heated at the rate of *ca.*  $1\text{ }^{\circ}\text{C min}^{-1}$  in darkness, the critical temperature ( $T_c$ ) varied extensively among species. The  $T_c$ 's of all 8 temperate-origin species ranged between  $40\text{--}46\text{ }^{\circ}\text{C}$  in winter (mean temperature  $16\text{--}19\text{ }^{\circ}\text{C}$ ), and between  $32\text{--}48\text{ }^{\circ}\text{C}$  in summer (mean temperature *ca.*  $30\text{ }^{\circ}\text{C}$ ). Those for 1 subtropical- and 12 tropical-origin  $C_3$  species ranged between  $25\text{--}44\text{ }^{\circ}\text{C}$  and  $35\text{--}48\text{ }^{\circ}\text{C}$ , and for 1 CAM and 4  $C_4$  species were  $41\text{--}47$  and  $45\text{--}46\text{ }^{\circ}\text{C}$ , respectively. Acclimating three  $C_3$  herbaceous plants at high temperature ( $33/28\text{ }^{\circ}\text{C}$ , day/night) for 10 d in winter caused their  $T_c$ 's rising to nearly the values measured in summer. When leaves were exposed to  $45\text{ }^{\circ}\text{C}$  for 20 min and then kept at room temperature in darkness for 1 h, a significant correlation between  $RF_{v/m}$  (the ratio of  $F_v/F_m$  before and after  $45\text{ }^{\circ}\text{C}$  treatment) and  $T_c$  was observed for all tested temperate-origin  $C_3$  species as well as tropical-origin CAM and  $C_4$  species. However,  $F_0$  and  $F_v/F_m$  of the tropical-origin  $C_3$  species were less sensitive to  $45\text{ }^{\circ}\text{C}$  treatment, regardless of a large variation of  $T_c$ ; thus no significant correlation was found between their  $RF_{v/m}$  and  $T_c$ . Thus  $T_c$  might not be a suitable index of heat tolerance for plants with wide range of environmental adaptation. Nevertheless,  $T_c$ 's of tropical origin  $C_3$  species, varying and showing high plasticity to seasonal changes and temperature treatment, appeared suitable for the estimation of the degree of temperature acclimation in the same species.

*Additional key words:*  $C_3$ ,  $C_4$ , and CAM plants; species differences in fluorescence; temperate origin; thermo-tolerance; tropical origin.

### Introduction

Photosynthesis apparatus is very sensitive to temperature (Björkman *et al.* 1980). The optimal temperature range of photosynthesis is usually different for plants grown at different temperature. Comparing with those growing in higher temperature conditions, plants growing in lower temperature (at higher latitude or elevation) have lower optimal temperature range for photosynthesis (Slatyer and Morrow 1977, Schwarz and Redmann 1989, Weng and Ueng 1997).

Chlorophyll (Chl) fluorescence parameters are widely used as indicators for functional changes of photosynthesis apparatus under temperature stress (Schreiber and Berry 1977, Yamada *et al.* 1996). Among Chl fluorescence parameters for estimating thermo-tolerance, the temperature-dependent increase in minimal fluorescence ( $F_0$ ) in the dark ( $F_0$ -T curve) has been routinely used (Schreiber and Berry 1977, Smillie and Nott 1979, Bilger

*et al.* 1984, Downton *et al.* 1984, Kitao *et al.* 2000, Knight and Ackerly 2002). In contrast to  $F_0$ -T curve, which measures  $F_0$  under fast temperature shifting (about  $1\text{ }^{\circ}\text{C min}^{-1}$ ), Yamada *et al.* (1996) proposed another parameter, ratios of  $F_0$ ,  $F_m$ , and  $F_v/F_m$ , which were obtained before and after high temperature ( $45\text{ }^{\circ}\text{C}$ ) treatment for 20 min.

For  $F_0$ -T curve, the increase in  $F_0$  occurs in two steps. First  $F_0$  increases slightly at lower temperature and then sharply at about  $40\text{--}50\text{ }^{\circ}\text{C}$  (Bilger *et al.* 1984, Seemann *et al.* 1986, Kitao *et al.* 2000, Braun *et al.* 2002, Knight and Ackerly 2002). The temperature at which  $F_0$  starts to increase sharply ( $T_c$ ) is correlated with a number of physiological factors that are related to high temperature tolerance, such as the decline in photosynthetic capacity (Schreiber and Berry 1977, Downton *et al.* 1984, Seemann *et al.* 1986) and irreversible tissue damage

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*Abbreviations:* Chl – chlorophyll;  $F_0$  – basic chlorophyll fluorescence;  $F_m$  – maximum chlorophyll fluorescence;  $F_v/F_m$  – potential efficiency of PS2; PPFD – photosynthetic photon flux density; PS2 – photosystem 2;  $T_c$  – temperature at the start of  $F_0$  sharp increase;  $T_p$  – temperature at maximum  $F_0$ .

(Bilger *et al.* 1984). Tropical plants typically have higher  $T_c$  than temperate plants, and temperate plants have higher  $T_c$  than alpine plants (Smillie and Nott 1979). The thermo-tolerance is highly plastic, and  $T_c$  would rise when plants grow at a higher temperature (Downton *et al.* 1984, Seemann *et al.* 1986, Königer *et al.* 1998, Knight and Ackerly 2002). These results have demonstrated that species or plants growing in warmer conditions would have greater intrinsic photosynthetic heat tolerance and higher  $T_c$ .

However, Knight and Ackerly (2002) reported that the heat tolerance, estimated from  $F_0$ -T curve, was not necessarily greater for species with warm-climate distri-

butions, when measured in a common environment. We also found that some plants of tropical origin had very low  $T_c$  (<35 °C), in contrast to plants of temperate origin.

Studies to compare the thermo-tolerance of plant species of tropical and temperate origins by different Chl fluorescence parameters have been rare. In the present study, 8 temperate- and 1 subtropical-origin  $C_3$  species as well as 17 tropical-origin species, including  $C_3$ ,  $C_4$ , and CAM plants, were used to elucidate their difference in thermo-tolerance, using both  $F_0$ -T curve and the difference in Chl fluorescence parameters, before and after high temperature treatment.

## Materials and methods

**Plants:** Eight species of temperate-origin  $C_3$  plants (Table 1) and 18 species of tropical- or subtropical-origin, including  $C_3$ ,  $C_4$ , and CAM plants (Table 2) grown in the garden or pots on the campus of the National Chung-Hsing University, Taichung, Taiwan (24°10'N, 78 m a.s.l.) were used. They received water and fertilizer regularly in pots and were exposed to full sunlight in both pots and garden. Their Chl fluorescence was measured in two seasons, *i.e.* January–February and July, 2003. The mean temperatures in Taichung were 16.4, 18.8, and 29.8 °C in January, February, and July of 2003, respectively.

In addition, in February three tropical-origin species, namely rice, sweet potato, and *Ipomoea aquatica*, were acclimated for 10 d in a growth cabinet. The photosynthetic photon flux density (PPFD) in the cabinet was 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Plants were irradiated for 13 h each day and the temperature was 33/28 °C (day/night).

**Measurement of temperature-dependent Chl fluorescence:** Attached (herbaceous plants) or detached (woody plants) fully expanded youngest leaves were linearly heated from room temperature to the final temperatures of 45–50 °C, in a growth cabinet with about 1 °C  $\text{min}^{-1}$  graduation in darkness. Measurement of the Chl fluorescence was taken every two minutes with a portable fluorometer (*Handy PEA*, *Hansatech*, UK). Leaf temperature was taken with copper-constantan thermocouples connected to the abaxial surface of the leaf.

$T_c$  was determined from the intersection point of two regression lines extrapolated from the slow and fast rising portion of the temperature-dependent basal fluorescence ( $F_0$ ) response (Fig. 1). Three to four leaves sampled from 1 (for some tree species) to 3 or 4 (for all herbaceous species) plants were measured. The result of each leaf was used as the statistical parameter for each replication.

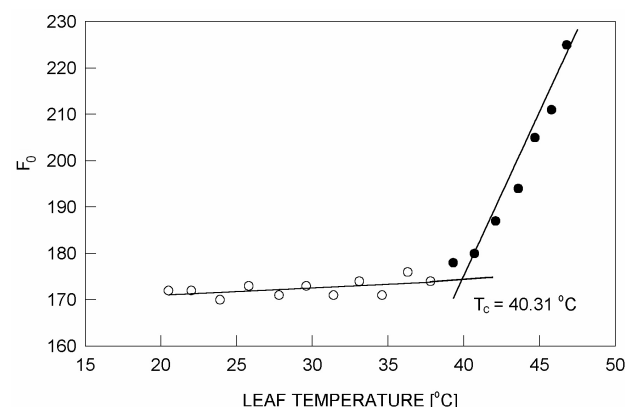


Fig. 1. Determination of the critical temperature ( $T_c$ , the temperature at which basic fluorescence  $F_0$  increased sharply when leaf was exposed to high temperature treatment at about 1 °C  $\text{min}^{-1}$  graduation in darkness) as the intersection point of two regression lines extrapolated from the slow and the fast rising portions of the temperature-dependent  $F_0$  response.

**Measurement of fluorescence before and after high temperature treatment:** Detached fully expanded youngest leaves were used. The Chl fluorescence of dark-adapted leaves was measured with a *Handy PEA* fluorometer with an excitation radiation of 1 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for 2 s at room temperature of *ca.* 23 °C in winter and 30 °C in summer. Then the leaves were incubated in a water bath in the dark at 45 °C and 100 % relative humidity for 20 min. Finally the fluorescence of leaves, which had been adapted in the dark at room temperature for 1 h, was measured again (Yamada *et al.* 1996).

Four leaves sampled from 1–4 plants were measured 6–8 times for each leaf. The average of each leaf was used as the statistical parameter of each replication.

## Results and discussion

It was reported that  $F_0$ -T curve in darkness increased slightly until the temperature went up to about 40–50 °C. Then  $F_0$  increased sharply until near-maximum, and the temperature when  $F_0$  rose to the maximum was about 46–63 °C (Bilger *et al.* 1984, Kuropatwa *et al.* 1992, Braun *et al.* 2002, Knight and Ackerly 2002). However, the temperature at which  $F_0$  began to rise sharply ( $T_c$ ) and up to maximum ( $T_p$ ) varied with species and environmental conditions (Kuropatwa *et al.* 1992, Braun *et al.* 2002, Knight and Ackerly 2002). In addition, Kuropatwa *et al.* (1992) reported that the  $F_0$ -T curve of barley leaves had two  $T_p$ 's, the first one around 51 °C and the second one around 62 °C. In the present study, the  $F_0$ -T curve under darkness varied with both species and seasons (for typical patterns see Fig. 2). Since the final temperature of measurement in our study was 45–50 °C,  $T_p$  of most tested species could not be determined. However, some tropical-origin species had very low  $T_c$  and  $T_p$ . As shown in Fig. 2A,  $T_c$  and  $T_p$  of *Ipomoea aquatica* measured in Jan.–Feb. were *ca.* 30 and 40 °C, respectively. The same tendency was also found in mango (data not shown). Fig. 2C also shows that in Jan.–Feb., rice leaves had very low  $T_c$  and  $T_p$ , *i.e.* 27 and 35 °C, respectively. In addition,  $F_0$  rose again up to higher than  $T_p$  when the temperature increased to above 45 °C (Fig. 2C). Perhaps rice leaves might have two  $T_p$ 's, and  $F_0$  of the second  $T_p$  would be higher than that of the first one. This result is different from that of barley leaves (Kuropatwa *et al.* 1992), in which  $F_0$  of the second  $T_p$  was lower than that of the first one. In addition, the temperatures when  $F_0$  of rice leaves rose to both first and second  $T_p$ 's were much lower than those for barley leaves (Kuropatwa *et al.* 1992). Fig. 2E,F also suggests that another tropical-origin woody species, *Pachira marrocarpa*, might have two  $T_c$ 's in measurements made in both seasons. But,  $F_0$  did not rise as sharply as in rice when the temperature was higher than  $T_c$ , especially in July, and it was difficult to distinguish  $T_p$ . Fig. 2 also suggests that the three species showed higher  $T_c$  in July than in Jan.–Feb.

The  $T_c$ 's of temperate-origin  $C_3$  species measured in two seasons are shown in Table 1, and those of subtropical- and tropical-origin species are shown in Table 2. The  $T_c$ 's of most tested temperate-origin species fell between 40–48 °C, but the  $T_c$  of *Brassica oleracea* was only 32 °C in July. The difference of  $T_c$ 's measured in winter and summer of the same temperate-origin species was less than 1.9 °C (Table 1). On the contrary, the  $T_c$ 's of subtropical- and tropical-origin species were 25–47 °C in Jan.–Feb. and 35–48 °C in July (Table 2). Among them, pineapple, a CAM plant, showed a higher  $T_c$ , with no significant difference between winter and summer. The  $T_c$ 's of 4  $C_4$  species (maize, sugar cane, and two of *Miscanthus*) were 41–44 °C in winter and 45–46 °C in summer; and for the same  $C_4$  species, the difference of  $T_c$ 's between winter and summer was 1.6–4.1 °C

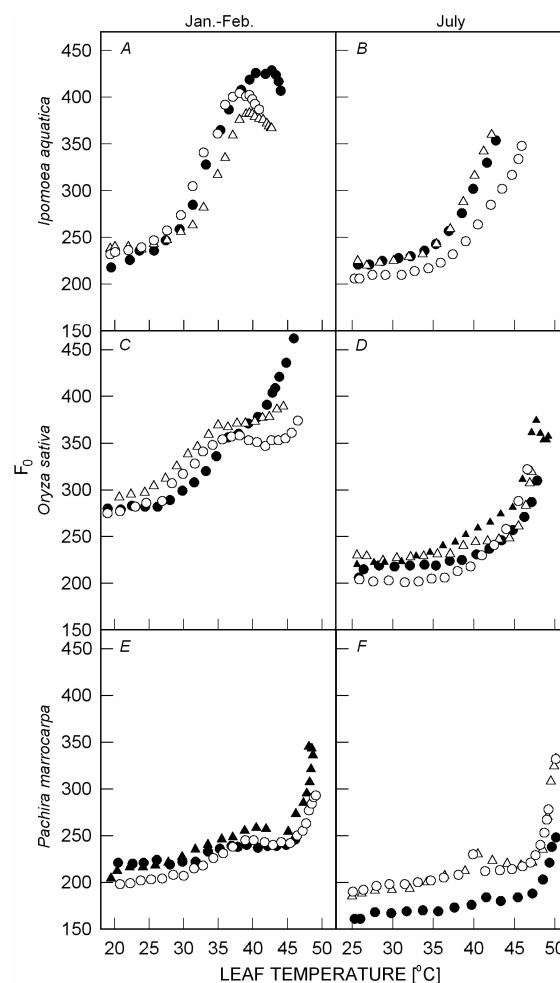


Fig. 2. Typical patterns of temperature-dependent basic fluorescence ( $F_0$ ) response to temperature increase at about 1 °C min<sup>-1</sup> graduation in darkness for different species in two seasons. Different symbols in a panel indicate different leaves (replications).

[2.49±1.40 (SD)]. On the contrary, the  $T_c$ 's of tropical-origin  $C_3$  species varied extensively with species, ranging between 25–44 °C in winter and 35–48 °C in summer (Table 2). In winter,  $T_c$ 's of only 2 species (papaya and *Acacia*) were as high as 43–44 °C with another one (guava) at 38 °C, the remaining species had very low  $T_c$ 's, from 25 to 32 °C. In summer,  $T_c$ 's of six species, *i.e.* rice, papaya, guava, avocado, longan, and *Acacia*, rose to 43–48 °C, those of two *Ipomoea* species and mango were 35–36 °C, and that of the remaining three species (*Pachira marrocarpa* and two *Ficus* species) was approximately 39 °C. All these results suggest that some tropical-origin  $C_3$  species have very low  $T_c$ , especially in winter, and for the same tropical-origin  $C_3$  species, the difference of  $T_c$ 's between winter and summer was 2.5–22.0 (9.45±5.95) °C.

Previous reports pointed out that  $T_c$ 's of plants would

rise when growing at high temperature (Downton *et al.* 1984, Seemann *et al.* 1986, Königer *et al.* 1998, Knight and Ackerly 2002). In this study, acclimating 3 C<sub>3</sub> herbaceous plants (rice and 2 *Ipomoea* species) at high temperature (33/28 °C, day/night) for 10 d in winter caused temperature acclimation.

Downton *et al.* (1984) reported that the difference of T<sub>c</sub>'s for summer annual plants growing at 28/21 and 43/32 °C was 5–7 °C, while under the same growing conditions that for winter annuals was 3–4 °C. Seemann *et al.* (1986) also stated that T<sub>c</sub>'s of 5 desert annual plants in the field rose by 6–9 °C from Feb. to May, and the

their T<sub>c</sub>'s rising to nearly the values measured in summer (Table 2). Since the mean temperature in January, February, and July of 2003 in Taichung was 16.4, 18.8, and 29.8 °C, respectively, the difference of T<sub>c</sub>'s measured in different seasons could be considered mainly due to the mean daily maximum temperature of this period increased by 12 °C. These results indicate that the plasticity of T<sub>c</sub>'s for summer and desert annual plants was higher than that for winter annuals. However, in our study, the difference of T<sub>c</sub>'s between two seasons for temperate-origin C<sub>3</sub> species was less than 2 °C, and that for tropical-origin 1 CAM, 4 C<sub>4</sub>, and 12 C<sub>3</sub> species was –0.75,

Table 1. T<sub>c</sub> and RF<sub>0</sub> of temperate-origin C<sub>3</sub> species in two seasons. Means±SE. T<sub>c</sub>: critical temperature, at which the basic fluorescence F<sub>0</sub> increased sharply when the leaf was exposed to about 1 °C min<sup>-1</sup> graduation in darkness; RF<sub>0</sub>: ratio of F<sub>0</sub> before and after treatment of leaves with high temperature (45 °C for 20 min and then kept in dark room for 1 h).

Family	Scientific name (common name)	T <sub>c</sub> [°C]	July	RF <sub>0</sub>	July
		Jun.-Feb.		Jun.-Feb.	
Brassicaceae	<i>Brassica napus</i> (rape)	40.41±0.78	–	1.91±0.17	–
Brassicaceae	<i>B. oleracea</i> L. var. <i>alboglabra</i>	–	31.81±0.45	–	2.08±0.46
Asteraceae	<i>Lactuca sativa</i> (lettuce)	41.61±0.17	–	1.40±0.06	–
Leguminosae	<i>Pisum sativum</i> (pea)	41.38±0.38	–	1.71±0.05	–
Rosaceae	<i>Rosa rugosa</i> (rose)	46.12±0.27	47.99±0.40	1.06±0.03	1.07±0.02
Rosaceae	<i>Prunus campanulata</i> (cherry)	42.09±0.52	42.87±0.44	1.16±0.02	1.07±0.02
Rosaceae	<i>Pyrus koehnei</i> (pear)	45.31±0.45	46.9±0.437	1.16±0.02	1.12±0.02
Betulaceae	<i>Alnus formosana</i> (Taiwan alder)	44.57 0.10	45.75±0.21	1.13±0.02	1.13±0.02

Table 2. T<sub>c</sub> and RF<sub>0</sub> of tropical- or subtropical-origin species in two seasons. Means±SE. T<sub>c</sub>: critical temperature, at which the basic fluorescence F<sub>0</sub> increased sharply when the leaf was exposed to about 1 °C min<sup>-1</sup> graduation in darkness; RF<sub>0</sub>: ratio of F<sub>0</sub> before and after treatment of leaves with high temperature (45 °C for 20 min and then kept in dark room for 1 h). #: Acclimated in a growth cabinet at high temperature (33/28°C, day/night) for 10 d; ##: subtropical-origin.

Family	Scientific name (common name, type)	T <sub>c</sub> [°C]	July	RF <sub>0</sub>	July
		Jan.-Feb.		Jan.-Feb.	
Bromeliaceae	<i>Ananas comosus</i> (pineapple, CAM)	47.19±0.99	46.44±0.92	0.98±0.04	0.98±0.05
Gramineae	<i>Zea mays</i> (maize, C <sub>4</sub> )	42.67±0.07	—	1.07±0.01	—
Gramineae	<i>Saccharum officinarum</i> (sugarcane, C <sub>4</sub> )	41.31±0.51	45.41±0.39	1.02±0.02	1.04±0.03
Gramineae	<i>Miscanthus transmorrisonensis</i> (C <sub>4</sub> )	43.52±1.54	45.24±0.13	0.99±0.01	1.05±0.02
Gramineae	<i>Miscanthus floridulus</i> (C <sub>4</sub> )	44.39±0.86	46.03±0.37	—	1.02±0.01
Gramineae	<i>Oryza sativa</i> (rice, cv. Taiken 14, C <sub>3</sub> )	27.02±1.03	42.90±0.85	1.09±0.03	1.13±0.03
		45.59±0.76 <sup>#</sup>			
Convolvulaceae	<i>Ipomoea batatas</i> (sweet potato, C <sub>3</sub> )	29.39±0.60	34.63±1.07	1.11±0.03	1.21±0.14
		33.59±0.28 <sup>#</sup>			
Convolvulaceae	<i>Ipomoea aquatica</i> (C <sub>3</sub> )	30.42±0.90	35.95±0.60	1.19±0.05	1.05±0.04
		36.91±0.84 <sup>#</sup>			
Caricaceae	<i>Carica papaya</i> (papaya, C <sub>3</sub> )	43.85±0.51	46.39±0.65	1.06±0.02	1.03±0.04
Myrtaceae	<i>Psidium guajava</i> (guava, C <sub>3</sub> )	37.74±0.71	43.88±0.56	1.08±0.02	1.07±0.02
Bombacaceae	<i>Pachira marrocarpa</i> (C <sub>3</sub> )	29.14±1.18	38.90±0.46	0.97±0.02	1.11±0.02
Anacardiaceae	<i>Mangifera indica</i> (mango, C <sub>3</sub> )	24.78±0.05	34.80±1.13	0.97±0.02	1.02±0.01
Lauraceae	<i>Persea americana</i> (avocado, C <sub>3</sub> )	32.00±0.37	48.47±0.33	1.08±0.06	1.06±0.01
Sapindaceae	<i>Euphoria longana</i> (longan, C <sub>3</sub> )	25.85±0.58	47.82±0.70	1.33±0.13	1.11±0.05
Leguminosae	<i>Acacia confusa</i> (C <sub>3</sub> )	43.25±0.09	46.00±0.52	1.03±0.04	1.15±0.13
Moraceae	<i>Ficus retusa</i> (C <sub>3</sub> )	29.46±0.61	39.20±1.43	1.06±0.01	1.03±0.03
Moraceae	<i>Ficus wightiana</i> (C <sub>3</sub> )	32.18±0.82	39.53±0.58	1.03±0.02	1.03±0.01
Rutaceae	<i>Citrus sinensis</i> (orange, C <sub>3</sub> ) <sup>##</sup>	36.71±0.38	35.83±0.06	1.06±0.01	1.02±0.02

2.49±1.40, and 9.45±5.95 °C, respectively. This result suggests that only tropical-origin C<sub>3</sub> species showed a higher plasticity of T<sub>c</sub> between winter and summer.

When leaves were exposed to high temperature (45 °C) for 20 min and then kept in dark room for 1 h, the ratio of F<sub>0</sub> thus measured to that before treatment (RF<sub>0</sub>) of temperate-origin species was 1.06–1.91 (1.32±0.23) in Jan.-Feb., and 1.07–2.08 (1.29±0.39) in July, respectively (Table 1). Among the species studied, some vegetable crops, *e.g.* pea and *Brassica*, showed very high RF<sub>0</sub>. On the contrary, RF<sub>0</sub>'s of tropical-origin C<sub>3</sub>, C<sub>4</sub>, and CAM species were 0.97–1.33 (1.07±0.27) and 0.98–1.21 (1.07±0.06), respectively, for winter and summer (Table 2). This result indicates that tropical-origin species had lower variation of RF<sub>0</sub> among species than temperate-origin species.

High temperature inhibits photosynthesis, and PS2 is very sensitive in photosynthesis apparatus (Berry and Björkman 1980, Weis and Berry 1988). Measured on

dark-acclimated leaves, F<sub>v</sub>/F<sub>m</sub> is an indicator of the potential photochemical efficiency of PS2 (Ball *et al.* 1994, Maxwell and Johnson 2000). Present study showed that when leaves were exposed to 45 °C for 20 min, the ratio of F<sub>v</sub>/F<sub>m</sub> before and after treatment (RF<sub>v/m</sub>) was closely related to that of RF<sub>0</sub>. A significant negative correlation between them was observed for all tested species when measurements were made either in winter or summer (Fig. 3). Among the tested temperate-origin C<sub>3</sub> species, some species, *e.g.* pea and *Brassica*, had RF<sub>v/m</sub> and T<sub>c</sub> lower than the tropical-origin CAM and C<sub>4</sub> species (Table 1, Fig. 3). Combining the data, measured in two seasons, for all tested temperate-origin C<sub>3</sub> species as well as tropical-origin CAM and C<sub>4</sub> species a significant correlation between RF<sub>v/m</sub> and T<sub>c</sub> was obtained (Fig. 4). On the contrary, in spite of high variation of their T<sub>c</sub>'s, the variation of RF<sub>0</sub> and RF<sub>v/m</sub> among tropical-origin C<sub>3</sub> species was as low as that among CAM and C<sub>4</sub> species; thus their RF<sub>v/m</sub>'s were not related to T<sub>c</sub>'s (Fig. 4).

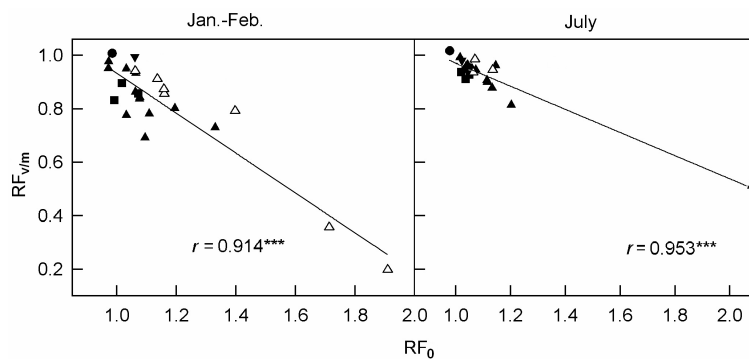


Fig. 3. Relationships between RF<sub>v/m</sub> and RF<sub>0</sub> for all tested species in two seasons. RF<sub>v/m</sub> and RF<sub>0</sub>: the ratios of F<sub>v</sub>/F<sub>m</sub> and F<sub>0</sub> before and after the leaves were exposed to high temperature (45 °C for 20 min and then kept in dark room for 1 h). Δ: temperate-origin C<sub>3</sub> species; ▼: subtropical-origin C<sub>3</sub> species; ▲, ■, ●: tropical-origin C<sub>3</sub>, C<sub>4</sub>, and CAM species. \*\*\*:  $p < 0.001$ .

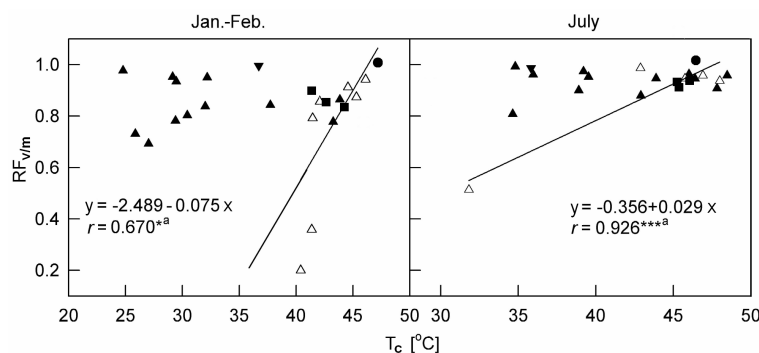


Fig. 4. Relationships between RF<sub>v/m</sub> and T<sub>c</sub> for tested species in two seasons. RF<sub>v/m</sub>: the ratios of F<sub>v</sub>/F<sub>m</sub> before and after the leaves were exposed to high temperature (45 °C for 20 min and then kept in dark room for 1 h); T<sub>c</sub>: critical temperature. Δ: temperate-origin C<sub>3</sub> species; ▼: subtropical-origin C<sub>3</sub> species; ▲, ■, ●: tropical-origin C<sub>3</sub>, C<sub>4</sub>, and CAM species. \* and \*\*\*:  $p < 0.05$  and  $p < 0.001$ , respectively; a: regression analysis excluded the data of tropical and subtropical-origin C<sub>3</sub> species.

The above results show that T<sub>c</sub> may not adequately reflect the heat tolerance of plants with wide range of environmental adaptation, *e.g.* plants of temperate- and tropical-origins. However, T<sub>c</sub> shows higher plasticity in

the same species in different seasons or under different temperature treatments, and thus may be suitable for estimating the degree of temperature acclimation in the same species.

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