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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 °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 40–46 °C in winter (mean temperature 16–19 °C), and between 32–48 °C in summer (mean temperature *ca*. 30 °C). Those for 1 subtropical- and 12 tropical-origin C_3 species ranged between 25–44 °C and 35–48 °C, and for 1 CAM and 4 C_4 species were 41–47 and 45–46 °C, respectively. Acclimating three C_3 herbaceous plants at high temperature (33/28 °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 °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 °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 °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 °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 °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 40–50 °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 distributions, 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 μmol m^{-2} 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 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.

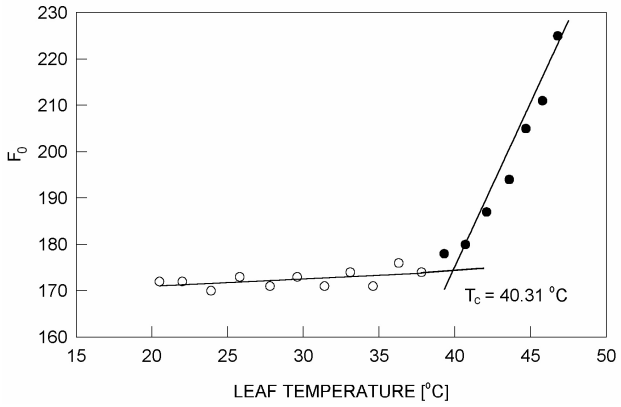

Fig. 1. Determination of the critical temperature (T_c, the temperature at which basic fluorescence F_0 increased sharply when leaf was exposed to high temperature treatment at about 1 °C min^{-1} graduation in darkness) as the intersection point of two regression lines extrapolated from the slow and 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 μmol m^{-2} 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. 2*A*, 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. 2*C* 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. 2*C*). 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. 2*E,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 [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.

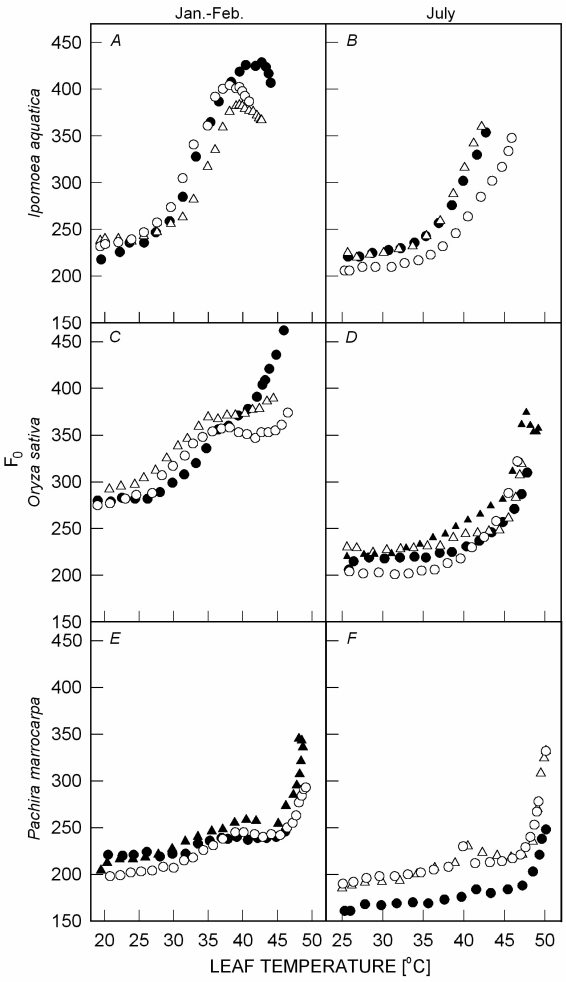

Fig. 2. Typical patterns of temperature-dependent basic fluorescence (F_0) response to temperature increase at about 1 °C min^{-1} graduation in darkness for different species in two seasons. Different symbols in a panel indicate different leaves (replications).

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_3 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_c'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_c's of 5 desert annual plants in the field rose by 6–9 °C from Feb. to May, and the their T_c'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_c'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_c's for summer and desert annual plants was higher than that for winter annuals. However, in our study, the difference of T_c's between two seasons for temperate-origin C_3 species was less than 2 °C, and that for tropical-origin 1 CAM, 4 C_4, and 12 C_3 species was –0.75,

Table 1. T_c and RF_0 of temperate-origin C_3 species in two seasons. Means±SE. T_c: critical temperature, at which the basic fluorescence F_0 increased sharply when the leaf was exposed to about 1 °C min^{-1} graduation in darkness; RF_0: ratio of F_0 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_c [°C] Jun.-Feb.	July	RF_0 Jun.-Feb.	July
Brassicaceae	*Brassica napus* (rape)	40.41±0.78	–	1.91±0.17	–
Brassicaceae	*B. oleracea* L. var. *alboglabra*	–	31.81±0.45	–	2.08±0.46
Asteraceae	*Lactuca sativa* (lettuce)	41.61±0.17	–	1.40±0.06	–
Leguminosae	*Pisum sativum* (pea)	41.38±0.38	–	1.71±0.05	–
Rosaceae	*Rosa rugosa* (rose)	46.12±0.27	47.99±0.40	1.06±0.03	1.07±0.02
Rosaceae	*Prunus campanulata* (cherry)	42.09±0.52	42.87±0.44	1.16±0.02	1.07±0.02
Rosaceae	*Pyrus koehnei* (pear)	45.31±0.45	46.9±0.437	1.16±0.02	1.12±0.02
Betulaceae	*Alnus formosana* (Taiwan alder)	44.57 0.10	45.75±0.21	1.13±0.02	1.13±0.02

Table 2. T_c and RF_0 of tropical- or subtropical-origin species in two seasons. Means±SE. T_c: critical temperature, at which the basic fluorescence F_0 increased sharply when the leaf was exposed to about 1 °C min^{-1} graduation in darkness; RF_0: ratio of F_0 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_c [°C] Jan.-Feb.	July	RF_0 Jan.-Feb.	July
Bromeliaceae	*Ananas comosus* (pineapple, CAM)	47.19±0.99	46.44±0.92	0.98±0.04	0.98±0.05
Gramineae	*Zea mays* (maize, C_4)	42.67±0.07	——	1.07±0.01	——
Gramineae	*Saccharum officinarum* (sugarcane, C_4)	41.31±0.51	45.41±0.39	1.02±0.02	1.04±0.03
Gramineae	*Miscanthus transmorrisonensis* (C_4)	43.52±1.54	45.24±0.13	0.99±0.01	1.05±0.02
Gramineae	*Miscanthus floridulus* (C_4)	44.39±0.86	46.03±0.37	——	1.02±0.01
Gramineae	*Oryza sativa* (rice, cv. Taiken 14, C_3)	27.02±1.03 45.59±0.76#	42.90±0.85	1.09±0.03	1.13±0.03
Convolvulaceae	*Ipomoea batatas* (sweet potato, C_3)	29.39±0.60 33.59±0.28#	34.63±1.07	1.11±0.03	1.21±0.14
Convolvulaceae	*Ipomoea aquatica* (C_3)	30.42±0.90 36.91±0.84#	35.95±0.60	1.19±0.05	1.05±0.04
Caricaceae	*Carica papaya* (papaya, C_3)	43.85±0.51	46.39±0.65	1.06±0.02	1.03±0.04
Myrtaceae	*Psidium guafava* (guava, C_3)	37.74±0.71	43.88±0.56	1.08±0.02	1.07±0.02
Bombacaceae	*Pachira marrocarpa* (C_3)	29.14±1.18	38.90±0.46	0.97±0.02	1.11±0.02
Anacardiaceae	*Mangifera indica* (mango, C_3)	24.78±0.05	34.80±1.13	0.97±0.02	1.02±0.01
Lauraceae	*Persea americana* (avocado, C_3)	32.00±0.37	48.47±0.33	1.08±0.06	1.06±0.01
Sapindaceae	*Euphoria longana* (longan, C_3)	25.85±0.58	47.82±0.70	1.33±0.13	1.11±0.05
Leguminosae	*Acacia confusa* (C_3)	43.25±0.09	46.00±0.52	1.03±0.04	1.15±0.13
Moraceae	*Ficus retusa* (C_3)	29.46±0.61	39.20±1.43	1.06±0.01	1.03±0.03
Moraceae	*Ficus wightiana* (C_3)	32.18±0.82	39.53±0.58	1.03±0.02	1.03±0.01
Rutaceae	*Citrus sinensis* (orange, C_3)##	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_3 species showed a higher plasticity of T_c 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_0 thus measured to that before treatment (RF_0) 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_0. Onthe contrary, RF_0's of tropical-origin C_3, C_4, 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_0 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_v/F_m 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_v/F_m before and after treatment ($RF_{v/m}$) was closely related to that of RF_0. 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_3 species, some species, *e.g*. pea and *Brassica*, had $RF_{v/m}$ and T_c lower than the tropical-origin CAM and C_4 species (Table 1, Fig. 3). Combining the data, measured in two seasons, for all tested temperate-origin C_3 species as well as tropical-origin CAM and C_4 species a significant correlation between $RF_{v/m}$ and T_c was obtained (Fig. 4). On the contrary, in spite of high variation of their T_c's, the variation of RF_0 and $RF_{v/m}$ among tropical-origin C_3 species was as low as that among CAM and C_4 species; thus their $RF_{v/m}$'s were not related to T_c's (Fig. 4).

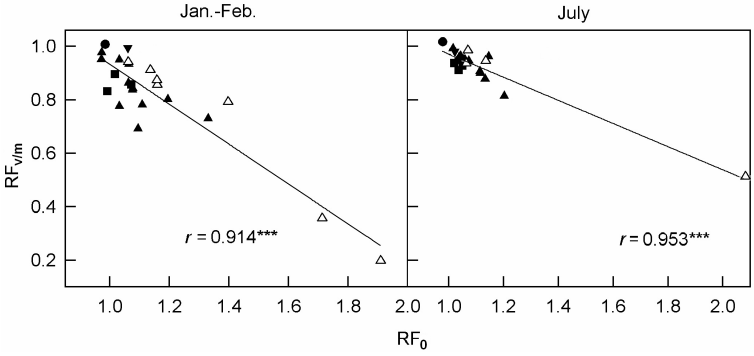

Fig. 3. Relationships between $RF_{v/m}$ and RF_0 for all tested species in two seasons. $RF_{v/m}$ and RF_0: the ratios of F_v/F_m and F_0 before and after the leaves were exposed to high temperature (45 °C for 20 min and then kept in dark room for 1 h). Δ: temperate-origin C_3 species; ▼: subtropical-origin C_3 species; ▲, ■, ●: tropical-origin C_3, C_4, and CAM species. ***: $p<0.001$.

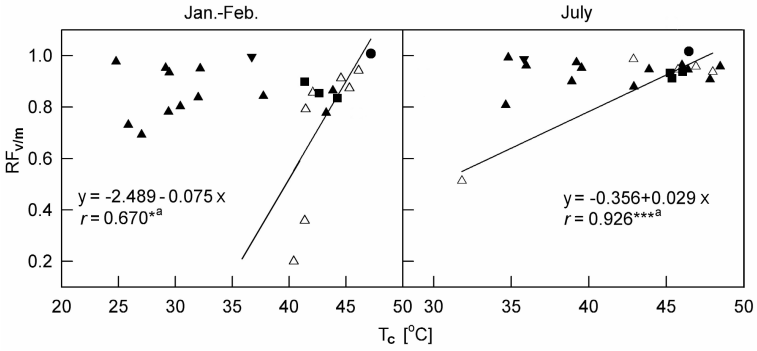

Fig. 4. Relationships between $RF_{v/m}$ and T_c for tested species in two seasons. $RF_{v/m}$: the ratios of F_v/F_m before and after the leaves were exposed to high temperature (45 °C for 20 min and then kept in dark room for 1 h); T_c: critical temperature. Δ: temperate-origin C_3 species; ▼: subtropical-origin C_3 species; ▲, ■, ●: tropical-origin C_3, C_4, and CAM species. * and ***: $p<0.05$ and $p<0.001$, respectively; a: regression analysis excluded the data of tropical and subtropical-origin C_3 species.

The above results show that T_c 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_c 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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