

Temperature acclimation of the photosynthetic apparatus in an evergreen shrub, *Nerium oleander*.

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Introduction

Temperature dependence of photosynthesis varies even in plants of the same species grown under different temperature conditions (Berry & Björkman 1980). In many species, optimal temperature of photosynthesis is lower in leaves grown under lower temperatures. So far, several hypotheses have been suggested on the mechanisms of temperature acclimation of photosynthesis: 1) physiological changes in some processes, including changes in heat stability of enzymes, 2) stomatal conductance for CO₂, 3) internal conductance for CO₂, and 4) changes in nitrogen partitioning among photosynthetic components. However, there seemed no authors who studied all of these factors in a single species. In the present study, we used an evergreen shrub, *Nerium oleander*. Although Badger et al. (1982) conducted a comprehensive biochemical study for this species, suggesting that difference in heat stability was a major factor in the temperature dependence of photosynthesis, gas exchange characteristics still remain to be studied.

Materials and methods

Nerium oleander was grown in growth cabinets. A halogen lamp provided light of 400-500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Temperature was maintained at 20 or 35°C. Relative humidity was adjusted to be 80%. Gas exchange was determined with a portable photosynthesis system (Li-6400, LiCor, USA). Chlorophyll fluorescence was determined with a fluorometer (PAM-2000, Waltz, Germany) and the quantum yield of the electron transport was calculated according to Genty et al. (1989). Nitrogen, chlorophyll (chl), and ribulose-1,5-bisphosphate carboxylase (RuBPCase) contents were determined according to Hikosaka and Terashima (1996).

Results and discussion

CO₂ dependence of the light-saturated photosynthetic rate at two temperatures (20 and 35°C) is shown in Fig. 1. Shape of the curve was close to Blackman-type (characterised by two linear lines), except for 20°C-grown leaves at 35°C which showed a less saturating curve. The photosynthetic rate at the ambient CO₂ (P₃₆), shown by arrows in the figure, was higher in 20°C-grown leaves at 20°C while it was similar between 20°C- and 35°C-grown leaves at 35°C. At 35°C, intercellular partial pressure of CO₂ (C_i) was lower in 20°C-grown leaves than in 35°C-grown leaves, which contributed to lowering P₃₆ of 20°C leaves at 35°C (Table 1).

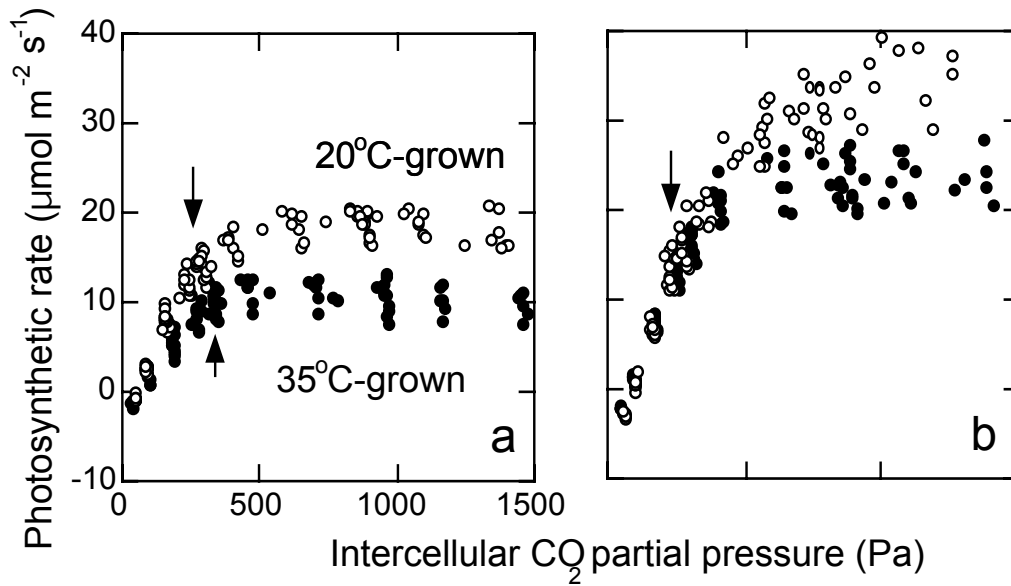


Figure 1. CO₂ dependence of photosynthetic rates of 20°C- and 35°C-grown leaves measured at 20°C (a) and 35°C (b). Arrows denote the rate at ambient CO₂ (36 Pa).

Table 1. Gas exchange characteristics of *Nerium oleander* leaves grown under different temperatures. Intercellular CO₂ partial pressure at ambient CO₂ (C_i), the CO₂ compensation point in the absence of day respiration (Γ^*), maximum rates of carboxylation ($V_{c_{max}}$), RuBP regeneration (J_{max}), and triose-phosphate utilisation (TPU), and their interrelationships.

Measurement temperature	20°C		35°C	
Growth temperature	20°C	35°C	20°C	35°C
C_i (Pa)	28.1 ± 0.9	33.0 ± 1.5	26.4 ± 1.8	30.1 ± 0.9
Γ^* (Pa)	4.00 ± 0.42	4.18 ± 0.20	6.31 ± 0.24	6.14 ± 0.62
$V_{c_{max}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	58 ± 6	36 ± 0	156 ± 4	109 ± 5
J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	122 ± 14	80 ± 2	215 ± 14	162 ± 8
TPU ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	6.1 ± 0.7	3.9 ± 0.1	11.6 ± 0.8	8.5 ± 0.4
$J_{max}/V_{c_{max}}$	2.1 ± 0.1	2.2 ± 0.1	1.4 ± 0.1	1.5 ± 0.0
TPU/ $V_{c_{max}}$ (x10)	1.06 ± 0.02	1.08 ± 0.04	0.74 ± 0.03	0.78 ± 0.01
J_{max}/TPU	20 ± 1	20 ± 1	18 ± 0	19 ± 0

Table 2. Nitrogen, chl, and RuBPCase content of *Nerium oleander* leaves grown under different temperatures.

Growth temperature	20°C	35°C
Nitrogen content (mol m^{-2})	0.15 ± 0.02	0.09 ± 0.01
Chlorophyll content (mmol m^{-2})	0.79 ± 0.08	0.57 ± 0.05
RuBPCase content (g m^{-2})	1.85 ± 0.22	1.03 ± 0.28

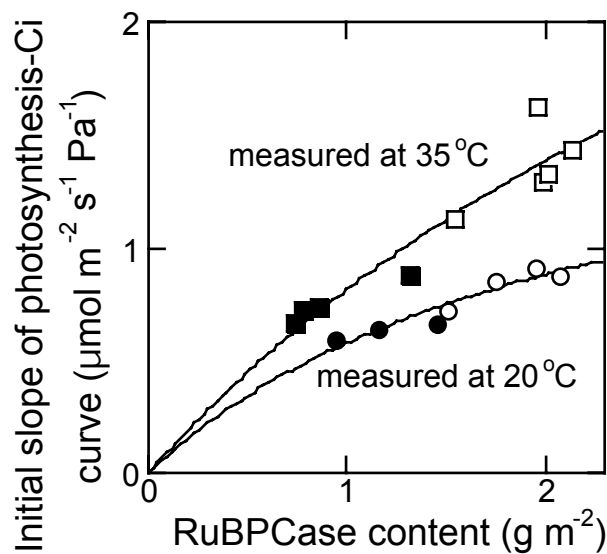


Figure 2. Relationship between the Initial slope of the photosynthesis- C_i curve. Open and closed symbol denotes 20°C- and 35°C-grown leaves, respectively.

Nitrogen, chl, and RuBPCase contents were higher in 20°C-grown leaves (Table 2). Figure 2 shows the initial slope (IS) of the CO_2 dependence of the photosynthetic rate plotted against RuBPCase content. The relationship between IS and RuBPCase content was expressed as a single curvilinear for each measurement temperature, suggesting that temperature response of RuBPCase activity did not differ between 20°C- and 35°C-grown leaves.

The CO_2 compensation point in the absence of day respiration (Γ^*) was also similar between the leaves (Table 1). We also compared rates of photosynthesis and the quantum yield of the electron transport to assess the effect of chloroplast CO_2 concentration (C_c). A higher ratio of photosynthesis to the yield indicates a higher CO_2 level at chloroplasts where a large fraction of reducing power produced by electron transport is utilized by photosynthesis. At a given C_i , the ratio of photosynthesis to the yield was similar at 20°C, and was slightly higher in 20°C-grown leaves at 35°C, but the difference was small (Fig. 3). This suggests that the C_c/C_i ratio was similar between 20°C- and 35°C-grown leaves. All of these results suggest that factors related with RuBPCase-limited rates do not contribute to changes in the temperature dependence of the photosynthetic rate.

The light-saturated rate of photosynthesis is limited by either of three steps: RuBPCase, RuBP regeneration, and triose-phosphate utilisation (TPU) (Sharkey 1985). To evaluate the capacity of these steps, CO_2 dependence of the photosynthetic rate was determined under three O_2 concentrations: data obtained at 10 and 20% O_2 was used to estimate the capacity of TPU, those obtained at 20% O_2 was for the capacity of RuBPCase, characterised in terms of $V_{c_{\max}}$ (Farquhar et al. 1980), and those obtained at 50% O_2 was for the capacity of RuBP

regeneration in terms of J_{\max} . Table 1 shows $V_{c\max}$, J_{\max} and TPU, and their interrelationships. $V_{c\max}$, J_{\max} , and TPU were always higher in 20°C-grown leaves. Among the interrelationships, only $J_{\max}/V_{c\max}$ and J_{\max}/TPU at 35°C were significantly different between 20°C- and 35°C-grown leaves (t -test, $P < 0.05$). This indicates that the balance between the three steps was different between 20°C- and 35°C-grown leaves at 35°C. Compared with $V_{c\max}$ and TPU, J_{\max} was relatively low in 20°C-grown leaves at 35°C.

In summary, compared with 35°C-grown leaves, 20°C-grown leaves had higher photosynthetic rates at 20°C due to larger amount of photosynthetic proteins. However, at 35°C, photosynthetic rates were similar between the leaves in spite of the difference in protein content. This was due to lowered C_i and RuBP regeneration capacity (J_{\max}). Temperature dependence of RuBPCase-limited photosynthetic rates and TPU was not affected by growth temperature. These results are consistent with Badger et al. (1982), who showed that several Calvin cycle enzymes of low- temperature grown leaves are not stable at higher temperatures in *Nerium oleander*.

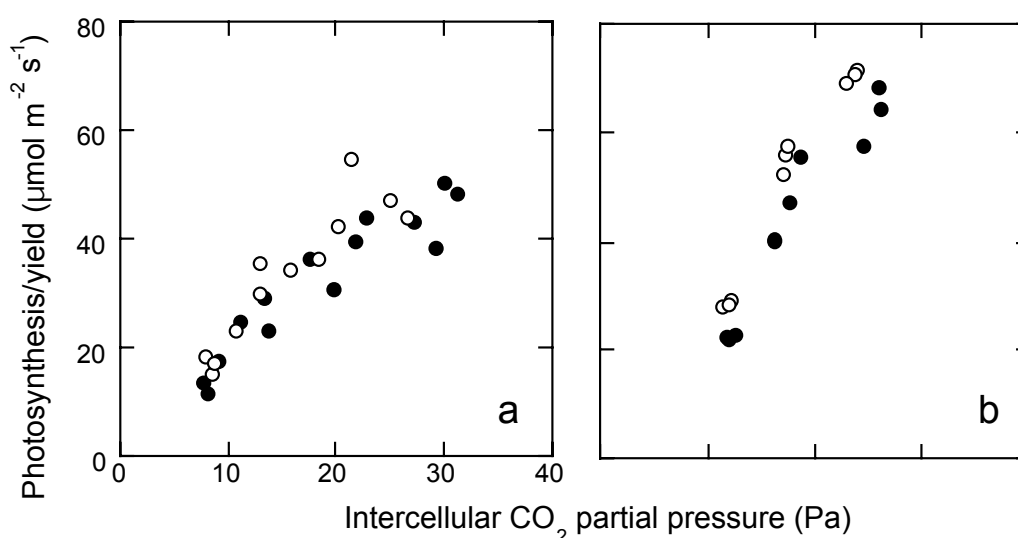


Figure 3. Ratio of photosynthetic rate to quantum yield of electron transport plotted against intercellular CO_2 partial pressure measured at 20°C (a) and 35°C (b). Open and closed circle denote 20°C- and 35°C-grown leaves, respectively.

However, these results are not necessarily consistent with previous studies for other species. Makino et al. (1994) found that low-temperature grown rice plants have lowered rates of RuBPCase-limited photosynthesis. Hikosaka et al. (1999) found that *Quercus myrsinaefolia*, an evergreen tree, alters temperature dependence of both rates of RuBPCase-limited photosynthesis and RuBP regeneration as well as the balance of these two processes. Bunce (2000) found that several summer annuals changes temperature dependence of both rates of RuBPCase-limited photosynthesis and RuBP regeneration without changes in the balance of these two processes. These inconsistent results may reflect the difference in temperature of the native habitat of the species. Temperature is one of the most important determinants for distribution of plants. Adaptation to different temperature regimes may require different types of mechanisms in temperature acclimation.

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