

Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate

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Abstract

Growth temperature alters temperature dependence of the photosynthetic rate (temperature acclimation). In many species, the optimal temperature that maximizes the photosynthetic rate increases with increasing growth temperature. In this minireview, mechanisms involved in changes in the photosynthesis–temperature curve are discussed. Based on the biochemical model of photosynthesis, change in the photosynthesis–temperature curve is attributable to four factors: intercellular CO₂ concentration, activation energy of the maximum rate of RuBP (ribulose-1,5-bisphosphate) carboxylation ($V_{c\max}$), activation energy of the rate of RuBP regeneration (J_{\max}), and the ratio of J_{\max} to $V_{c\max}$. In the survey, every species increased the activation energy of $V_{c\max}$ with increasing growth temperature. Other factors changed with growth temperature, but their responses were different among species. Among these factors, activation energy of $V_{c\max}$ may be the most important for the shift of optimal temperature of photosynthesis at ambient CO₂ concentrations. Physiological and biochemical causes for the change in these parameters are discussed.

Key words: Activation energy, gas exchange, limitation, limiting step, model, nitrogen use, optimal temperature, photosynthetic acclimation, temperature response.

Introduction

With the predicted increase in global air temperature induced by the greenhouse effect, plant responses to increasing temperature have become a major area of concern

(Gunderson *et al.*, 2000; Rustad *et al.*, 2001). For modelling of photosynthesis, many studies have used the biochemical model of Farquhar *et al.* (1980), which mechanistically and realistically describes photosynthetic responses to environmental variables. However, many modelling studies have ignored intra- and interspecific difference in photosynthetic responses to temperature. One of the reasons is insufficient information on the full parameterization of the temperature response of the model (Leuning, 2002; Medlyn *et al.*, 2002a, b).

In most plants, as a direct response to temperature, the light-saturated rates of photosynthesis are low at extreme low and high temperatures and have an optimum at intermediate temperature. With changes in growth temperature many plants show considerable phenotypic plasticity in their photosynthetic characteristics. In general, plants grown at higher temperature have a higher optimal temperature of photosynthetic rate (Berry and Björkman, 1980). For example, Slatyer (1977) found a linear relationship between optimal and growth temperature with a slope of 0.34 °C °C⁻¹ in *Eucalyptus pauciflora*, i.e. the optimal temperature increased by *c.* 1 °C with an increase in growth temperature by 3 °C. Similar slopes were observed in *Oxyria digyna* (Billings *et al.*, 1971) and in *Ledum groenlandicum* (Smith and Hadley, 1974). Battaglia *et al.* (1996) reported 0.59 and 0.35 °C °C⁻¹ for *Eucalyptus globulus* and *E. nitens*, respectively. Cunningham and Read (2002) studied four temperate and four tropical evergreen species and found an interspecific difference in the relationship. In one of the temperate species (*Eucryphia lucida*), the optimal temperature was independent of growth temperature. The other seven species showed significant dependence, but the slope differed among species from 0.10 °C to 0.48 °C °C⁻¹.

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Changes in the temperature dependence of photosynthesis may be ascribed to changes in the activity and amount of photosynthetic components and/or CO₂ concentration in the carboxylation site. However, the response of each factor to temperature seems to differ among species (Berry and Björkman, 1980; Badger *et al.*, 1982; Ferrar *et al.*, 1989; Makino *et al.*, 1994; Hikosaka *et al.*, 1999; Yamasaki *et al.*, 2002). In this minireview, mechanisms involved in the acclimational changes in the photosynthesis–temperature curve, based on the biochemical model of C₃ photosynthesis (Farquhar *et al.*, 1980; von Caemmerer, 2000) are discussed. Four parameters are raised in the model, which potentially cause the change in temperature dependence of photosynthetic rates. Using published and unpublished data, the contribution of each parameter to photosynthetic acclimation in actual plants was assessed. The biochemical background of the changes in the parameters is also discussed. This work focuses on the temperature range where plants can grow and reproduce and acclimation to stressful temperatures (i.e. freezing, chilling, and very high temperatures) is outside the scope.

Theory

In the biochemical model of C₃ photosynthesis, the photosynthetic rate is limited either by the RuBP (ribulose-1,5-bisphosphate) carboxylation or by the RuBP regeneration (Farquhar *et al.*, 1980). The limiting step is different depending on the CO₂ concentration. At low CO₂ concentrations, RuBP is saturated and carboxylation of RuBP is the limiting step of photosynthesis. The photosynthetic rate (P_c) is expressed as a function of intercellular CO₂ concentration (C_i):

$$P_c = \frac{V_{c \max}(C_i - \Gamma^*)}{C_i + K_c(1 + O/K_o)} \quad (1)$$

where $V_{c \max}$ is the ‘apparent’ maximal velocity of RuBP carboxylation, K_c and K_o are the Michaelis–Menten constants of Rubisco for CO₂ and O₂, respectively, O is the O₂ concentration, and Γ^* is the CO₂ compensation point in the absence of day respiration.

Although Equation 1 is based on Rubisco kinetics, it involves other properties. First, C_i is not the same as the CO₂ concentration at the carboxylation site (C_c). C_c can be determined with several methods, concurrent measurement of gas exchange and carbon isotope discrimination (von Caemmerer and Evans, 1991) or chlorophyll fluorescence (Harley *et al.*, 1992a), although use of these methods for field-grown plants is not simple. Due to a significant resistance in CO₂ diffusion from intercellular spaces to stroma, C_c is *c.* 70% of C_i (von Caemmerer and Evans, 1991; Evans and von Caemmerer, 1996). K_c and K_o in Equation 1 are adjusted to values including the effect of internal CO₂ conductance and thus differ from their true values (von

Caemmerer *et al.*, 1994). Second, for catalysis, Rubisco needs to be activated with CO₂ and Mg²⁺. The activation state of Rubisco changes in response to light, CO₂ concentration, and other environmental factors (Perchorowicz *et al.*, 1981; Sage *et al.*, 1988; Kanечи *et al.*, 1996; Feller *et al.*, 1998). Regulation of activation is complex and involves the protein Rubisco activase (Salvucci and Crafts-Brandner, 2004a). Thus P_c is affected by Rubisco kinetics, Rubisco activation state, and CO₂ diffusion within the leaf. In spite of the complexity, Equation 1 clearly demonstrates the CO₂ dependence of photosynthetic rate at low C_i (von Caemmerer and Farquhar, 1981).

At high CO₂ concentrations, RuBP is not saturated and the photosynthetic rate (P_r) is limited by RuBP regeneration. Under light-saturated conditions P_r is expressed as

$$P_r = \frac{J_{\max}(C_i - \Gamma^*)}{4C_i + 8\Gamma^*} \quad (2)$$

where J_{\max} is the ‘apparent’ maximum rate of RuBP regeneration expressed as the rate of electron transport. The RuBP regeneration process involves electron transport, ATP synthesis, and Calvin cycle processes other than carboxylation. Although Equation 2 implies that P_r is limited by electron transport, the limiting step of RuBP regeneration at saturated light is not clear, as discussed later. It is probable that the limiting step of RuBP regeneration changes depending on leaf temperature. In the present study, the limitation by triose-phosphate utilization (TPU) (Sharkey, 1985; Sage, 1990) is not included in the analyses, because of the difficulty in distinguishing TPU limitation from RuBP limitation in the CO₂ response curve of photosynthesis (but it will be discussed later).

The rate of photosynthesis (P) that is realized is the minimum of the two,

$$P = \min(P_c, P_r) \quad (3)$$

Temperature dependence of the parameters is fitted using the Arrhenius model if it increases exponentially:

$$f(T_k) = f(25) \exp \left[\frac{E_a(T_k - 298)}{298RT_k} \right] \quad (4)$$

where $f(25)$ is the value of f at 25 °C, E_a is the activation energy of f , R is the universal gas constant (8.314 J mol⁻¹ K⁻¹) and T_k is leaf temperature in K. A peak model is often applied if deactivation at high temperatures is substantial:

$$g(T_k) = \frac{g(25) \exp \left[\frac{H_a(T_k - 298)}{298R(T_k + 25)} \right] \left\{ 1 + \exp \left[\frac{298\Delta S - H_d}{298R} \right] \right\}}{1 + \exp \left[\frac{\Delta S T_k - H_d}{T_k R} \right]} \quad (5)$$

where H_a is the activation energy, H_d is the energy of deactivation, and ΔS is an entropy term (Johnson *et al.*, 1942; von Caemmerer, 2000; Medlyn *et al.*, 2002b).

In the present study, the effect of dark respiration (day respiration) is ignored, although it sometimes has

significant effects on the temperature dependence of net photosynthetic rates. Although the values of K_c , K_o , and Γ^* may be slightly different across species and growth conditions, the values have not been determined for each species. In the present study, as in many previous studies, it is assumed that K_c , K_o , and Γ^* are not affected by growth conditions or by species (but it will be discussed later). Changes in the temperature dependence of P are ascribed to changes in (i) C_i , (ii) E_a of $V_{c \max}$, (iii) E_a of J_{\max} , and (iv) the ratio of J_{\max} to $V_{c \max}$. In the following sections, how these factors change with growth temperature and their potential contribution to the photosynthesis–temperature curve will be discussed.

Intercellular CO_2 concentration

Temperature dependence of photosynthesis is sensitive to the CO_2 concentration; the optimal temperature increases with CO_2 concentration (Fig. 1a; Berry and Björkman, 1980). Two factors are involved in this shift of optimal temperature (Kirschbaum and Farquhar, 1984). One is the shift of the limiting step. In many species, as discussed later, the optimal temperature of P_r is higher than that of P_c (Kirschbaum and Farquhar, 1984; Hikosaka *et al.*, 1999). Since RuBP regeneration limits photosynthesis at higher CO_2 concentrations, the optimal temperature is high at high CO_2 concentrations. The other is related to the kinetics of Rubisco, which has a large effect on P_c . At low CO_2 concentrations, the carboxylation rate is less sensitive to temperature because an increase in K_c partly cancels the increase in $V_{c \max}$. Furthermore, the photorespiration rate increases with temperature because Γ^* increases (Brooks and Farquhar, 1985). These effects are smaller at higher CO_2 concentrations, leading to an increase in the optimal temperature of P_c . Figure 1b shows the calculated CO_2 dependence of the optimal temperature maximizing P_c . The optimal temperature increases by *c.* $0.05 \text{ }^\circ\text{C}$ per $1 \text{ } \mu\text{mol mol}^{-1} \text{ CO}_2$, although the increment decreases with increasing CO_2 concentration.

Temperature dependence of C_i potentially affects the temperature dependence of photosynthesis. The optimal temperature is low if C_i decreases with increasing leaf temperature. Some studies showed that C_i decreases with increasing temperature in a leaf (Mooney *et al.*, 1978; Ferrar *et al.*, 1989). However, it has been shown that stomatal conductance is more sensitive to vapour pressure deficit (VPD) than to temperature. Leuning (1995) suggested that stomatal conductance is regulated so as to maintain the ratio of C_i to C_a (air CO_2 concentration) constant, irrespective of temperature if VPD is constant. If leaf temperature is increased with a constant water vapour pressure, then VPD increases with leaf temperature, which may decrease C_i .

Effects of growth temperature on C_i are different among species; in some studies C_i decreased with decreasing growth temperatures (Williams and Black, 1993; Hikosaka

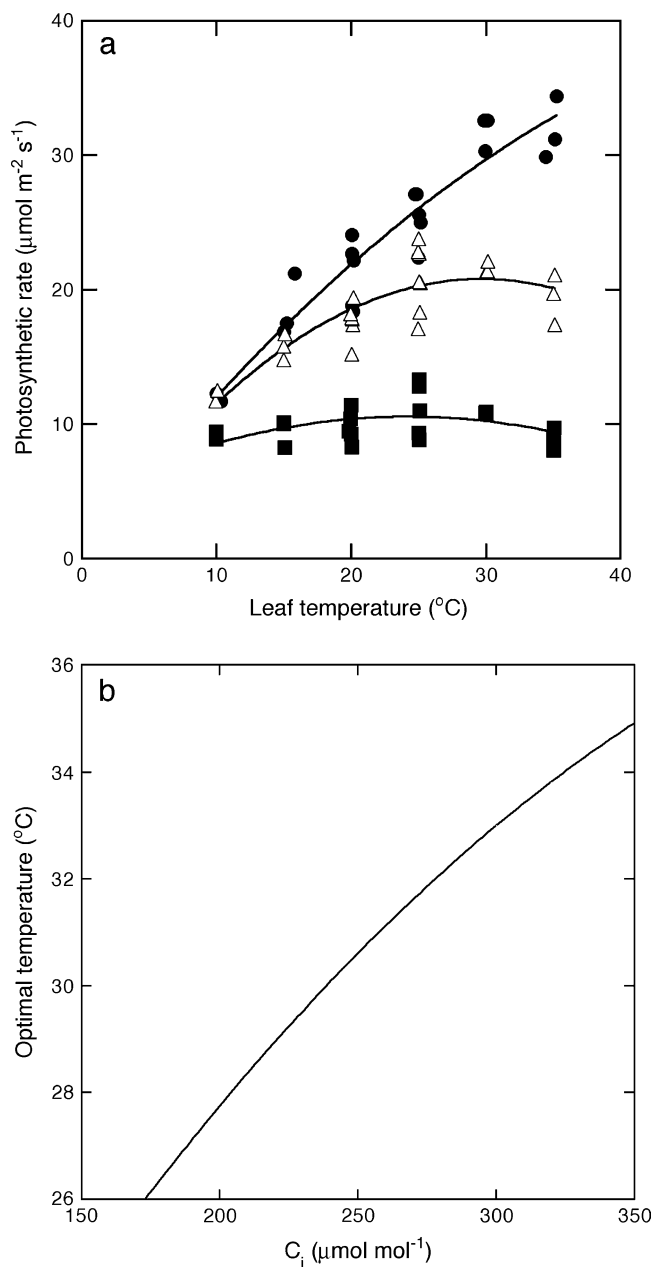


Fig. 1. Effect of CO_2 concentration on temperature dependence of photosynthesis. (a) Photosynthetic rate of *Plantago asiatica* grown at $15 \text{ }^\circ\text{C}$ as a function of leaf temperature. Squares, triangles, and circles denote rates determined at 200 , 370 , and $1000 \text{ } \mu\text{mol mol}^{-1} \text{ CO}_2$, respectively. Data points are fitted by two-dimensional polynomial. (b) Calculated relationship between the optimal temperature of RuBP carboxylation-limited photosynthesis (P_c) and intercellular CO_2 concentration (C_i). Equation 1 was used for the calculation. Kinetic constants followed Bernacchi *et al.* (2001).

et al., 1999; Hikosaka, 2005) but not in others (Hendrickson *et al.*, 2004). Ferrar *et al.* (1989) showed that two out of six *Eucalyptus* species had a low C_i when they were grown at low temperature, but four species did not show such tendencies. A large difference in C_i between leaves grown at different temperatures was found in *Quercus*

myrsinaefolia; 230 and 300 $\mu\text{mol mol}^{-1}$ in leaves grown at 15 °C and 30 °C, respectively (Hikosaka *et al.*, 1999), which might cause a shift of optimal temperature by 3 °C.

Temperature dependence of RuBP carboxylation-limited photosynthesis

In vitro Rubisco activity at saturating CO_2 exponentially increases with temperature (Jordan and Ogren, 1984). Similarly, in many species, $V_{c\text{max}}$ determined at a leaf-level ('apparent' $V_{c\text{max}}$) exponentially increases from 15 °C to 30 °C, but the deactivation is often substantial at very high temperature (Harley and Tenhunen, 1991; Leuning, 2002; Medlyn *et al.*, 2002b; Han *et al.*, 2004). In *Plantago asiatica*, deactivation was not obvious until 40 °C so the Arrhenius model (Fig. 2a) was applied. The activation energy, E_{aV} , is a measure of temperature dependence of P_c . E_{aV} has been reported to increase with growth temperature (Fig. 2a; Hikosaka *et al.*, 1999; Yamori *et al.*, 2005). Figure 3a shows the relationship between E_{aV} and growth temperature obtained from published and unpublished data. There was a large variation in E_{aV} among species, but in each species, E_{aV} consistently increased with growth temperature. It is notable that the slope is similar among species, suggesting that it is a general response to growth temperature.

As E_{aV} increases, the optimal temperature of P_c at ambient CO_2 increases with temperature (Fig. 2b). Figure 3b shows the calculated optimal temperature for P_c as a function of E_{aV} . The optimal temperature increases by 0.54 °C per 1 $\text{kJ mol}^{-1} E_{aV}$ (of course, the optimal temperature is not a simple function of E_{aV} if the deactivation is substantial). In this survey, the relationship between E_{aV} and growth temperature implies that with a 10 °C increase in growth temperature the E_{aV} increases by 10 kJ mol^{-1} (Fig. 3a). Combining Fig. 3a and b, the slope of the relationship between optimal and growth temperature is expected to be 0.54 °C °C⁻¹. This is close to the values obtained in previous studies (see Introduction).

Several mechanisms may be involved in the change in E_{aV} . The first one is the internal CO_2 conductance. As mentioned above, C_i is not the same as CO_2 concentration at the carboxylation site (C_c). The C_c to C_i ratio may vary among leaves (Terashima *et al.*, 2005). If the C_c to C_i ratio is low, the optimal temperature for P_c decreases and the E_{aV} will be calculated to be low. Makino *et al.* (1994) studied the relationship between gas exchange and Rubisco activity in rice (*Oryza sativa*) grown at different temperature. They found that the photosynthetic rate per unit Rubisco at a low C_i was low in leaves grown at low temperature. As Rubisco was not inactivated, they argued that C_c was lower in leaves grown at lower temperature. However, in *Nerium oleander*, a simultaneous measurement of gas exchange and chlorophyll fluorescence suggested that C_c was not different between leaves grown at

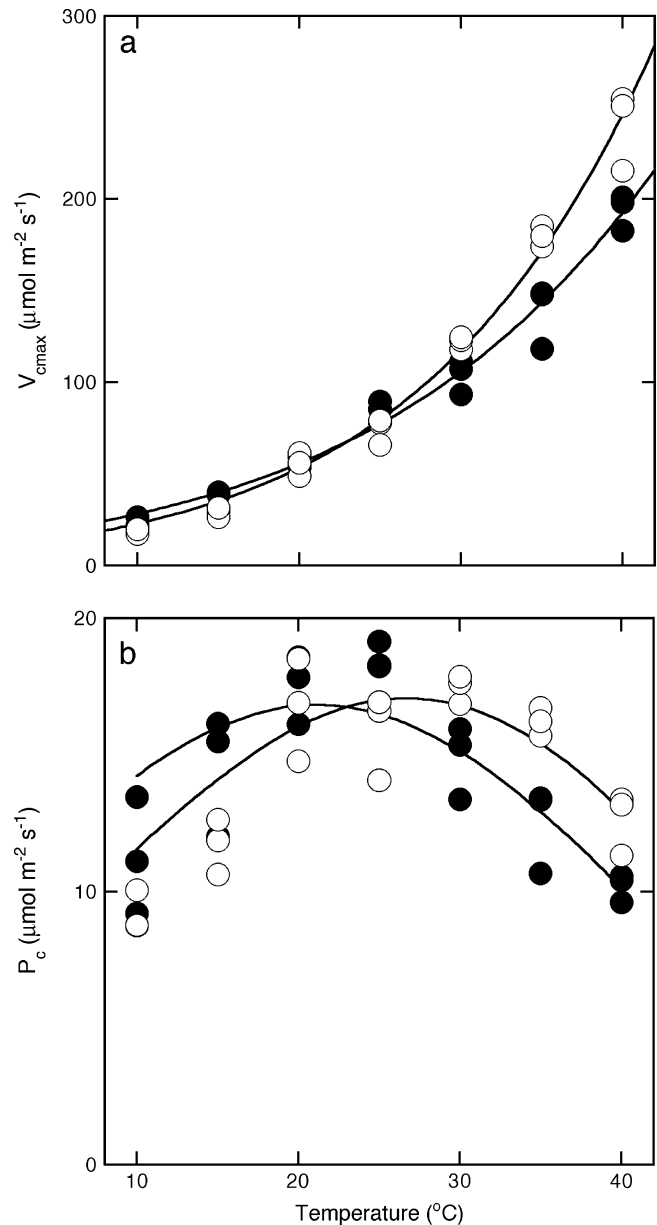


Fig. 2. Relationship between RuBP carboxylation-limited photosynthesis and leaf temperature. (a) $V_{c\text{max}}$ as a function of leaf temperature. Data were obtained from *Plantago asiatica* leaves grown at 15 °C (closed circles) and 30 °C (open circles) (K Ishikawa, unpublished data) and fitted with the Arrhenius model (Equation 4). Activation energy (E_{aV}) was 47.2 and 58.4 kJ mol^{-1} for leaves grown at 15 °C (closed circles) and 30 °C (open circles), respectively. (b) The rate of RuBP carboxylation-limited photosynthesis (P_c) at 280 $\mu\text{mol mol}^{-1} C_i$ as a function of leaf temperature. Points and lines were calculated from the points and the lines shown on Fig. 2a with Equation 1, respectively.

20 °C and 35 °C (Hikosaka and Hirose, 2001). Bernacchi *et al.* (2002) determined the temperature dependence of internal CO_2 conductance in tobacco (*Nicotiana tabacum*) leaves, which increased with increasing temperature with a temperature coefficient (Q_{10}) of 2.2 and had a maximum at 35–37.5 °C. Therefore, the photosynthetic rate above a leaf temperature of 40 °C may be suppressed by a lowered C_c .

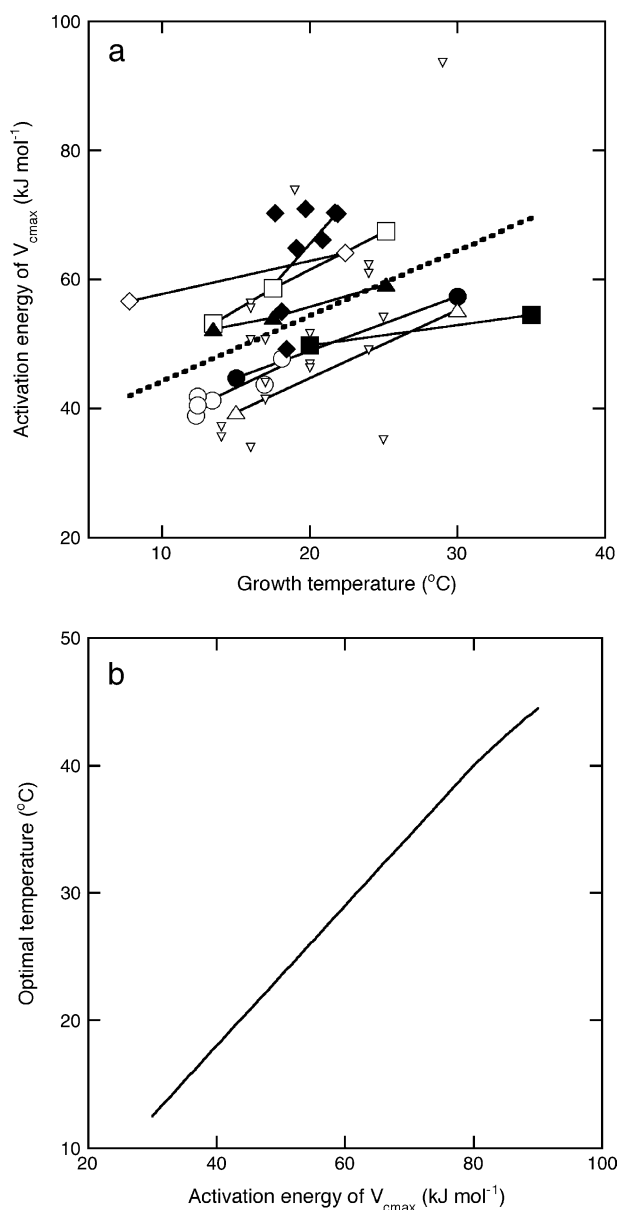


Fig. 3. (a) Relationship between activation energy of V_{cmax} (E_{av}) and growth temperature. Plants grown at controlled environment: closed circles, *Plantago asiatica* (data from K Ishikawa, unpublished results; see Fig. 2); closed squares, *Nerium oleander* (data from Hikosaka and Hirose, 2001), open triangles, *Quercus myrsinaefolia* (data from Hikosaka *et al.*, 1999). Plants grown in a seasonal environment: open circles, canopy leaves of *Quercus crispula* in a temperate forest (data from K Hikosaka, unpublished results); open squares, potted plants of *Polygonum cuspidatum* (data from Onoda *et al.*, 2005b); closed triangles, potted seedlings of *Fagus crenata* (data from Onoda *et al.*, 2005b); closed diamonds, top leaves of a rice canopy (data from A Borjigidai, unpublished results); open diamonds, current year leaves of *Aucuba japonica* grown at an experimental garden (data from O Muller, unpublished results). The data of V_{cmax} at high temperature were not included for the calculation of E_{av} if the deactivation was obvious. Literature surveys by Medlyn *et al.* (2002b) are shown as small triangles (a single point denotes one species). Continuous lines are for data points from each species. The thick dotted line denotes regression for all the data points ($y=34.1+1.01x$, $r=0.45$, $P<0.001$). (b) Calculated relationship between the optimal temperature of P_c and E_{av} . Equation 1 was used for the calculation assuming $280 \mu\text{mol mol}^{-1}$ for C_i and $65.33 \text{ kJ mol}^{-1}$ for E_{av} . Other kinetic constants followed Bernacchi *et al.* (2001).

The second candidate is the activation state of Rubisco. It has been reported that the activation state of Rubisco decreases at high temperature (Weis, 1981; Kobza and Edwards, 1987). Crafts-Brandner and Salvucci (2000) showed that, when leaf temperature exceeded 35°C , the photosynthetic rate in cotton was lower than that expected from Rubisco kinetics. The decrease in photosynthesis is ascribed to a decrease in Rubisco activation state (Law and Crafts-Brandner, 1999; Crafts-Brandner and Salvucci 2000; Salvucci and Crafts-Brandner, 2004a). Inactivation of Rubisco at high temperature may involve a decrease in activity of Rubisco activase (Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004a) and an increase in the synthesis of xylulose-1,5-bisphosphate, the catalytic misfire product, which inactivates Rubisco (Salvucci and Crafts-Brandner, 2004b).

In cotton grown at 28°C , inactivation of Rubisco is obvious only at leaf temperatures higher than 35°C (Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004a). The optimal temperature of P_c at ambient CO_2 is lower than 35°C in most of species, therefore Rubisco activation state may be less effective at the temperature that is lower than the optimum. However, for Antarctic hairgrass (*Deschampsia antarctica*), Salvucci and Crafts-Brandner (2004c) showed that inactivation occurred when leaf temperature exceeded 20°C , which was responsible for the decrease in the optimal temperature. Thus the activation state may have a significant effect on temperature dependence of photosynthesis in some species. Change in the activity of Rubisco activase is possibly involved in the temperature acclimation of photosynthesis. Law *et al.* (2001) showed that heat stress induces the synthesis of a new form of Rubisco activase in cotton. The difference in the heat stability between the two isoforms of Rubisco activase can be responsible for the change in photosynthesis–temperature curves (Law and Crafts-Brandner, 1999). However, experimental results suggest that activation state of Rubisco is not involved in temperature acclimation in *Nerium oleander* (Badger *et al.*, 1982) and rice (Makino *et al.*, 1994).

There may be several populations of Rubisco that respond differently to temperature (Yamori *et al.*, 2005). The balance between the two populations changes with growth temperature that, in turn, changes the E_{av} . Higher plants have only a single copy per chloroplast genome of the large subunit gene, but the small subunit genes constitute a multigene family ranging from 2 to 12 members (Gutteridge and Gatenby, 1995). Different combinations of the large and small subunit may produce a different nature of Rubisco.

Kinetic parameters of Rubisco (K_c , K_o , Γ^*) have been evaluated for only a limited number of species, and therefore this limited data set of the kinetic parameters has been used for modelling of photosynthesis. However, recently it has been suggested that the kinetic parameters

are different among species (Galmés *et al.*, 2005). Bunce (1998) reported that Γ^* increased with decreasing growth temperature in wheat and barley. Its generality and contribution to temperature dependence are unclear.

Temperature dependence of RuBP regeneration-limited photosynthesis

J_{\max} at a leaf level ('apparent' J_{\max}) can be assessed with several methods: gas exchange (Farquhar *et al.*, 1980), O_2 evolution at saturating CO_2 (Yamasaki *et al.*, 2002), and chlorophyll fluorescence analysis at saturating CO_2 (Niinemets *et al.*, 1999). In many species, deactivation of J_{\max} occurs at high temperature (Fig. 4a; Harley and Tenhunen, 1991; Leuning, 2002; Medlyn *et al.*, 2002b). The reduction of J_{\max} at high temperature affects the temperature dependence of P_r (Fig. 4b).

A shift in the optimal temperature for apparent J_{\max} with growth temperature was observed in some species (Fig. 4a; Badger *et al.*, 1982; Yamasaki *et al.*, 2002), but not in others (Armond *et al.*, 1978; Mitchell and Barber, 1986; Sage *et al.*, 1995). Furthermore the slope of the curve below the optimal temperature increases with growth temperature in many studies (Armond *et al.*, 1978; Badger *et al.*, 1982; Mitchell and Barber, 1986; Sage *et al.*, 1995; Hikosaka *et al.*, 1999; Yamasaki *et al.*, 2002). In *Plantago asiatica*, the H_a of the apparent J_{\max} in the peak model significantly increased with growth temperature (Fig. 4a). However, this pattern was not general in the data set of the survey (data not shown).

Changes in the heat tolerance in components of the RuBP regeneration process have been shown by many studies. Badger *et al.* (1982) showed that the thermal stability of various Calvin cycle enzymes changes with growth temperature in *Nerium oleander*. For example, exposure of leaves to 45 °C for 10 min decreased Ru5P (ribulose-5-phosphate) kinase activity in leaves grown at 20 °C by 50%, but did not affect leaves grown at 45 °C. Using chlorophyll fluorescence analysis, many studies have shown that the thermostability of photosystem II changes with growth temperature (Armond *et al.*, 1978; Berry and Björkman, 1980; Yamasaki *et al.*, 2002; Haldimann and Feller, 2005). However, it is unclear what components determine the temperature dependence of J_{\max} . Although it has been considered that electron transport limits the RuBP regeneration rate (Farquhar *et al.*, 1980; Kirschbaum and Farquhar, 1984; von Caemmerer, 2000), temperature dependence of the electron transport rate *in vitro* (e.g. the Hill activity) is different from that of the apparent J_{\max} in several studies. For example, in pea (*Pisum sativum*) leaves, E_a of the O_2 evolution rate increased with growth temperature, but the Hill activity was not affected by growth temperature (Mitchell and Barber, 1986). In *Nerium oleander*, the optimal temperature of photosynthetic rate at high CO_2 increased with growth temperature, while the optimal

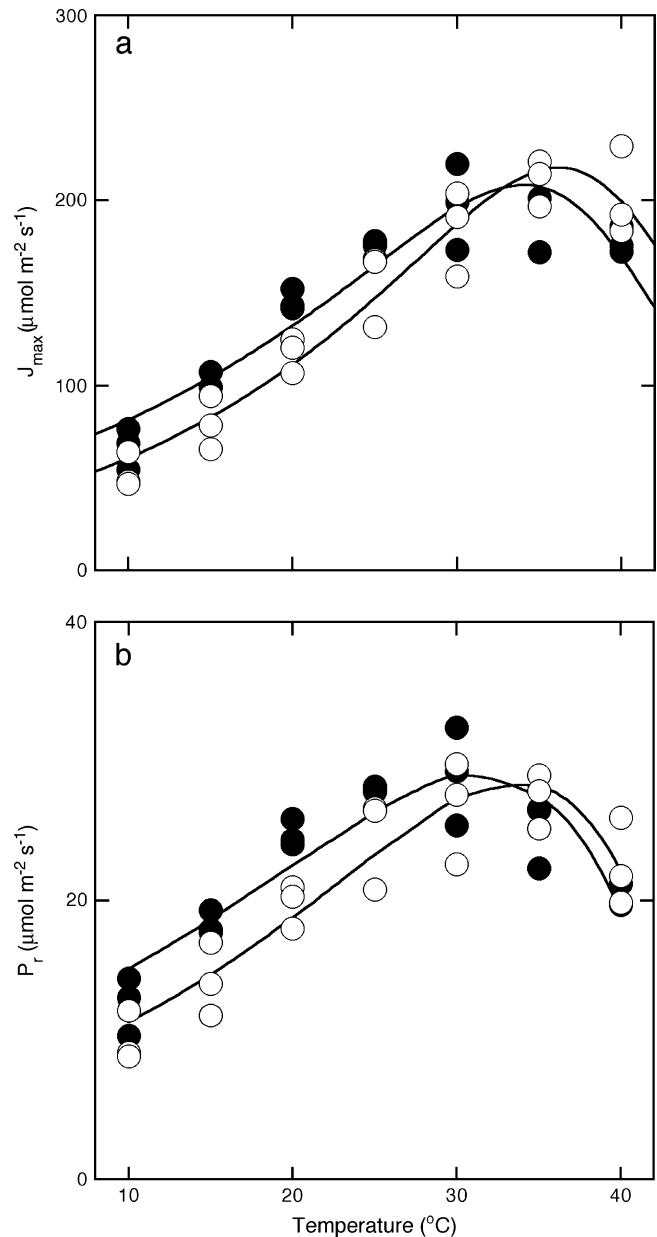


Fig. 4. Relationship between RuBP regeneration-limited photosynthesis and leaf temperature. Symbols are as Fig. 2. (a) J_{\max} as a function leaf temperature. Data points were fitted with the peak model (Equation 5) with the assumption that the energy of deactivation (H_d) = 200 kJ mol⁻¹ (Medlyn *et al.*, 2002b). Activation energy (H_a) was 33.8 and 42.0 kJ mol⁻¹ for leaves grown at 15 °C and 30 °C, respectively. The entropy term (ΔS) was 638 and 636 J K⁻¹ mol⁻¹ for leaves grown at 15 °C and 30 °C, respectively. (b) The rate of RuBP regeneration-limited photosynthesis (P_r) at 280 μmol mol⁻¹ C_i as a function of leaf temperature. Points and lines were calculated from the points and lines shown on Fig. 4a with Equation 2, respectively.

temperature of the Hill activity did not change (Badger *et al.*, 1982). Badger *et al.* (1982) suggested that stroma FBPase (fructose-1,6-bisphosphatase) was the limiting step in photosynthesis at high CO_2 in *Nerium oleander*. In wheat (*Triticum aestivum*), on the other hand, temperature dependence of the Hill activity and photosystem II activity

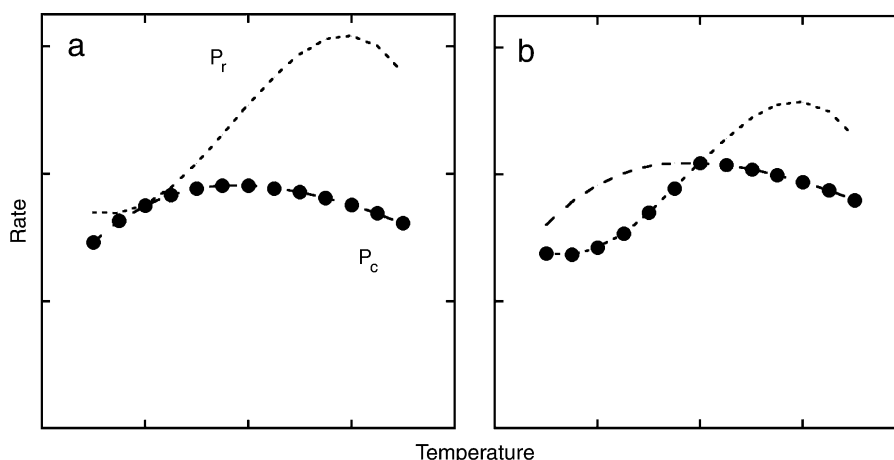


Fig. 5. A scheme illustrating the shift in optimal temperature of photosynthesis by the alteration in the ratio of J_{\max} to $V_{c\max}$. Photosynthetic rate (circles) is limited by the lower rate of P_r (dotted line) and P_c (broken line). P_r has a higher optimal temperature than P_c . (a) If the J_{\max} to $V_{c\max}$ ratio is high, the photosynthesis–temperature curve has a low optimal temperature. (b) if the J_{\max} to $V_{c\max}$ ratio is low, the optimal temperature shifts from a low to a high temperature with the alteration in limiting step.

were similar to that of the O_2 evolution rate (Yamasaki *et al.*, 2002). These facts suggest that the limiting step for the RuBP regeneration process is different among species.

Triose-phosphate utilization (TPU) is the third potential limiting step for light-saturated photosynthesis (Sharkey, 1985; Sage, 1990). It has often been believed that TPU limits photosynthesis only at very high CO_2 concentrations (Sage, 1994), but Labate and Leegood (1988) showed that TPU limits photosynthesis under normal CO_2 concentrations at lower temperature in barley (*Hordeum vulgare*) leaves. When photosynthesis is limited by TPU, the photosynthetic rate does not depend on the CO_2 concentration. Since P_r also becomes less sensitive to CO_2 concentration at low temperatures, CO_2 dependence of photosynthesis is not a good indicator to identify which of TPU or RuBP regeneration limits photosynthesis. O_2 sensitivity is useful because of different O_2 sensitivity between P_r and TPU-limited photosynthesis (Sharkey, 1985; Sage, 1990). Harley *et al.* (1992b) showed that the TPU-limited photosynthetic rate in cotton leaves had a temperature dependence that was similar to the temperature dependence of the apparent J_{\max} .

The balance between carboxylation and regeneration of RuBP

Temperature dependences of P_c and P_r at normal CO_2 concentration are generally different from each other (Kirschbaum and Farquhar, 1984; Hikosaka *et al.*, 1999). Therefore the temperature dependence of the photosynthetic rate changes depending on the limiting step. Furthermore, the balance between carboxylation and regeneration of RuBP potentially affects the temperature dependence of photosynthesis (Farquhar and von Caemmerer, 1982; Hikosaka, 1997; Onoda *et al.*, 2005b). Figure 5 illustrates

the effect of balance between the two processes on the temperature dependence of photosynthesis. At a normal CO_2 concentration, as mentioned above, P_c is less temperature-dependent and has a lower optimal temperature than P_r (Figs 2b, 4b). When plants increase P_r relative to P_c (i.e. higher J_{\max} to $V_{c\max}$ ratio), the optimal temperature of photosynthesis decreases (Fig. 5a), and vice versa (Fig. 5b).

From a literature survey of 109 species Wullschlegel (1993) showed a strong correlation between J_{\max} and $V_{c\max}$, suggesting that the balance between carboxylation and regeneration of RuBP is constant, irrespective of species and growth conditions. However, Hikosaka *et al.* (1999) showed that *Quercus myrsinaefolia*, an evergreen tree, alters the J_{\max} to $V_{c\max}$ ratio depending on the growth temperature. When the plants are grown at high temperature, the photosynthetic rate at $350 \mu\text{mol mol}^{-1} CO_2$ was limited by RuBP carboxylation above $22^\circ C$ and by RuBP regeneration below $22^\circ C$, while it was limited by RuBP carboxylation at any temperature in plants grown at a low temperature (Fig. 6). Similar changes in the J_{\max} to $V_{c\max}$ ratio have been observed in *Polygonum cuspidatum* (Onoda *et al.*, 2005a), spinach (Yamori *et al.*, 2005), and *Plantago asiatica* (Hikosaka, 2005).

However, there are also many species that did not show growth temperature-dependent changes in the J_{\max} to $V_{c\max}$ ratio: eight annual species (Bunce, 2000), *Pinus pinaster* (Medlyn *et al.*, 2002a), *Nerium oleander* (Hikosaka and Hirose, 2001), *Fagus crenata* (Onoda *et al.*, 2005b), and *Quercus crispula* (K Hikosaka, unpublished data). Why do some species alter the J_{\max} to $V_{c\max}$ ratio while others do not? If the temperature dependence of P_c and P_r are similar to each other, a change in the J_{\max} to $V_{c\max}$ ratio does not alter the temperature dependence of photosynthesis (Hikosaka, 1997). Whether or not P_c and P_r have a similar temperature dependence may be ascribed to the temperature

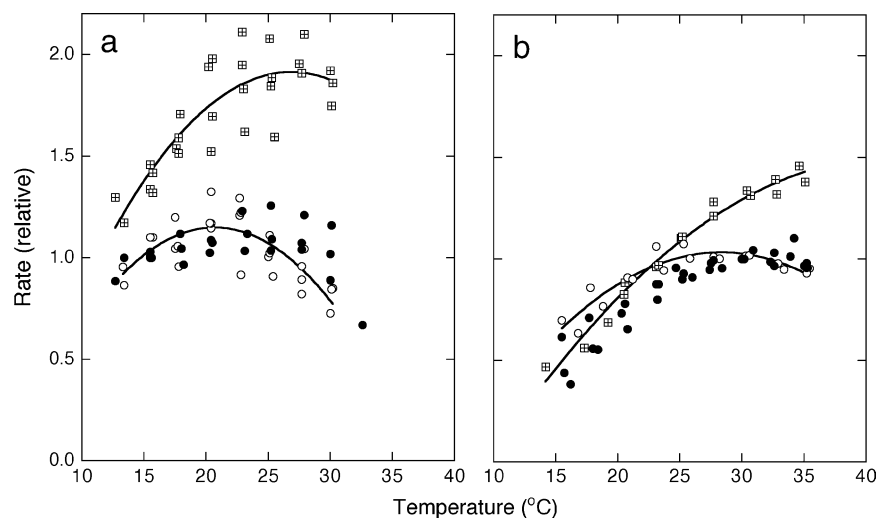


Fig. 6. Comparison of the photosynthetic rate and the potential rates of carboxylation (P_c) and regeneration (P_r) of RuBP at $350 \mu\text{mol mol}^{-1}$ CO_2 for *Quercus myrsinaefolia* leaves grown at 15°C (a) and 30°C (b). Closed circles, measured photosynthetic rate; open circles, calculated P_c ; squares, calculated P_r . Relative values normalized at growth temperature (15°C and 30°C) are shown. Fitted curves are two-dimensional polynomial. Redrawn from Hikosaka *et al.* (1999) with kind permission from Blackwell Publishing.

response of $V_{c \max}$ and J_{\max} (Onoda *et al.*, 2005b). Plants with a relatively low activation energy of J_{\max} (H_{aj}) have a temperature response of P_r similar to that of P_c . Onoda *et al.* (2005b) found that *Fagus crenata* with a relatively low H_{aj} did not alter the J_{\max} to $V_{c \max}$ ratio depending on growth temperature, while *Polygonum cuspidatum* with a relatively high H_{aj} altered the ratio.

Which limits photosynthesis, P_c or P_r ?

At a normal CO_2 concentration (*c.* $370 \mu\text{mol mol}^{-1}$), P_c and P_r are close to each other, but generally P_r is slightly higher than P_c (i.e. photosynthesis is limited by RuBP carboxylation) (Fig. 7a). In particular, photosynthesis at the optimal temperature is limited by P_c , irrespective of growth temperature (Figs 6, 7a; Hikosaka *et al.*, 1999). Therefore the changes in temperature dependence of photosynthesis may be explained mainly by $V_{c \max}$. An increase in the optimal temperature of photosynthesis is ascribed to the increase in E_{av} . RuBP regeneration is not substantial and may be responsible only when P_r is lower than P_c , which is often observed when photosynthesis is determined at temperatures lower than the growth temperature (Fig. 6b).

At an elevated CO_2 concentration (e.g. doubled CO_2 concentrations), on the other hand, photosynthesis is generally limited by RuBP regeneration (Fig. 7b; Sage, 1990, 1994). Thus temperature dependence of J_{\max} and the J_{\max} to $V_{c \max}$ ratio have a large effect on temperature dependence of photosynthesis. Onoda *et al.* (2005a) found that autumn leaves of *Polygonum cuspidatum* had a higher J_{\max} to $V_{c \max}$ ratio than summer leaves, irrespective of growth CO_2 concentration. Therefore, when photosynthetic rates were compared at the growth CO_2 concentration, the stimulation

in photosynthetic rate by elevated CO_2 was higher in autumn leaves. This result indicates that temperature acclimation affects the CO_2 response of photosynthesis.

Nitrogen partitioning in the photosynthetic apparatus under different growth temperatures

As nitrogen is a limiting resource of plant growth in many ecosystems, efficient use of nitrogen is believed to contribute to plant fitness. Since about half of leaf nitrogen is allocated to the photosynthetic apparatus, photosynthetic acclimation has been analysed in terms of nitrogen partitioning among photosynthetic components (Evans, 1989; Hikosaka and Terashima, 1995; Hikosaka, 2004). For example, shade leaves allocate more nitrogen to chlorophyll–protein complexes for light harvesting, while sun leaves have more nitrogen in Calvin cycle enzymes and electron carriers to achieve high photosynthetic capacity at high light (Boardman, 1977; Chow and Anderson, 1987; Evans, 1987; Terashima and Evans, 1988; Hikosaka, 1996; Hikosaka and Terashima, 1996; Makino *et al.*, 1997; Muller *et al.*, 2005a). Nitrogen reallocation from a non-limiting to a limiting process contributes to the efficient use of nitrogen in the photosynthetic apparatus (Evans, 1989; Hikosaka and Terashima, 1995; Hikosaka, 1997).

The temperature-dependent changes in the ratio of J_{\max} to $V_{c \max}$ may be explained with the change in nitrogen partitioning in the photosynthetic apparatus. In *Polygonum cuspidatum*, leaves grown at low temperature had a higher ratio of cytochrome *f* to Rubisco (Onoda *et al.*, 2005a). A similar result was also obtained for spinach (Yamori *et al.*, 2005). In *Plantago asiatica*, the relationship between Rubisco and leaf nitrogen content was not affected

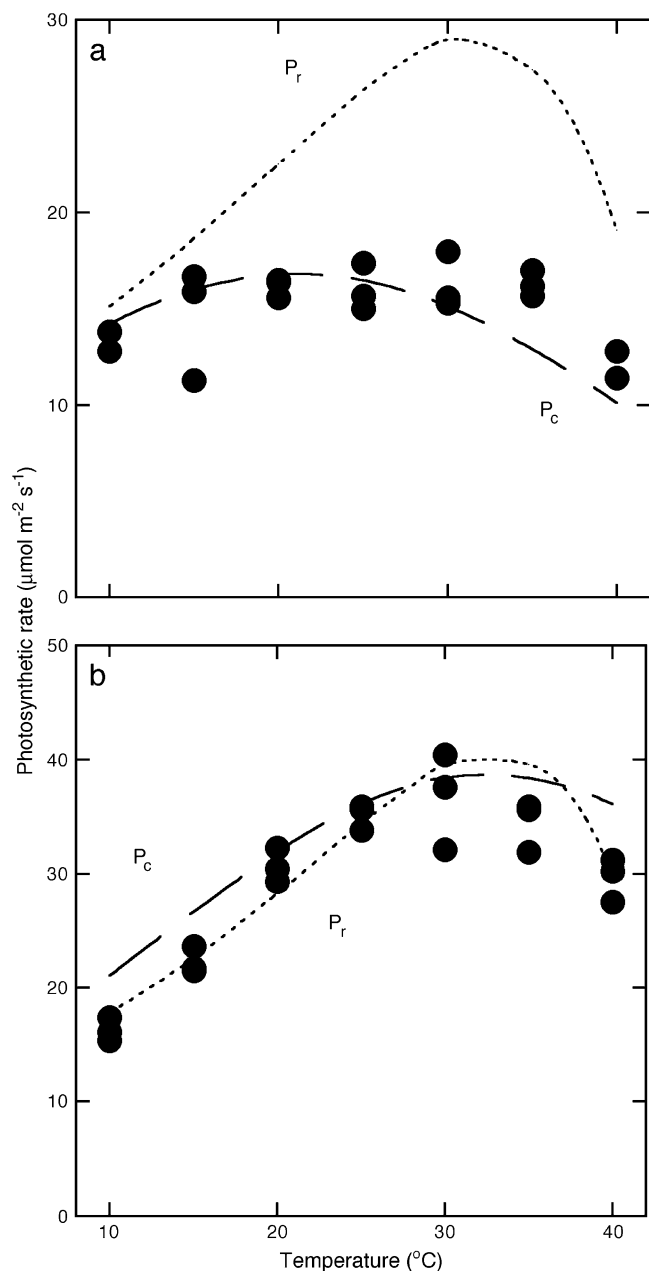


Fig. 7. Comparison of the photosynthetic rate and the potential rates of carboxylation (P_c) and regeneration (P_r) of RuBP at 370 (a) and 1000 $\mu\text{mol mol}^{-1}$ CO_2 (b) for *Plantago asiatica* leaves grown at 15 °C (K Ishikawa, unpublished data). Data points are measured photosynthetic rate, and lines are P_c and P_r calculated from temperature dependence of $V_{c\text{max}}$ (Fig. 2a) and J_{max} (Fig. 4a), respectively.

by growth irradiance and temperature, but low growth temperature increased the stroma FBpase level (Hikosaka, 2005). These results suggest that plants with a flexible J_{max} to $V_{c\text{max}}$ ratio invest more nitrogen in the RuBP regeneration process at lower growth temperature.

Using a model of nitrogen partitioning in the photosynthetic apparatus, Hikosaka (1997) predicted that the nitrogen use efficiency of photosynthesis is maximized when the photosynthetic rate is co-limited at the growth

temperature (i.e. $P_c=P_r$). In *Quercus myrsinaefolia* (Hikosaka *et al.*, 1999) and *Plantago asiatica* (Hikosaka, 2005), the P_r to P_c ratio at the growth temperature was 1.2–1.3, slightly higher than the optimum, but irrespective of growth temperatures. This suggests that plants regulate nitrogen partitioning to maintain a constant P_r to P_c ratio at growth temperature.

Photosynthetic rate at growth temperature

Temperature acclimation involves changes in the absolute photosynthetic rate. When compared among plants grown at various temperatures, the highest photosynthetic rate at a leaf temperature tended to be found in the plant grown at the same temperature (Slatyer, 1977; Mooney *et al.*, 1978; Berry and Björkman, 1980; Badger *et al.*, 1982; Hikosaka, 2005; Yamori *et al.*, 2005). Plants may realize the best performance at their growth temperature. In *Nerium oleander*, two mechanisms were involved in the regulation of photosynthetic rates in temperature acclimation (Badger *et al.*, 1982). First, to achieve higher photosynthetic rates at low temperature, low-temperature-grown leaves had a higher amount of photosynthetic proteins. Second, high-temperature-grown leaves had a higher heat tolerance of some Calvin cycle enzymes, which enabled higher photosynthetic rates at high temperatures.

Higher amounts of photosynthetic proteins in low-temperature-grown leaves have also been reported in many studies (Holaday *et al.*, 1992; Huner *et al.*, 1993, 1998; Steffen *et al.*, 1995; Strand *et al.*, 1999; Hikosaka, 2005). It may be a compensatory response to low temperature, which decreases enzyme activity. Interestingly, in some species, the photosynthetic rate at the growth temperature tends to be similar irrespective of growth temperature (Berry and Björkman, 1980). For example, *Plantago asiatica* had a photosynthetic rate of 19.0 and 19.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in leaves grown at 15 °C and 30 °C, respectively (Hikosaka, 2005). This suggests that temperature acclimation is a homeostatic response to maintain the photosynthetic rate at the growth condition.

Recently Muller *et al.* (2005b) discussed temperature response in absolute photosynthetic rates in relation to nitrogen use. The ecological and evolutionary significance of the environmental response in leaf nitrogen content per unit area have been analysed from the viewpoint of the optimization theory. Daily carbon gain as a function of leaf nitrogen content shows a saturating curve and there is a leaf nitrogen content that maximizes daily carbon gain per unit nitrogen (nitrogen use efficiency: Hirose, 1984; Hirose and Werger, 1987). The optimal leaf nitrogen content is higher at higher growth irradiance and there is a strong correlation among the optimal and actual nitrogen content (Hirose and Werger, 1987). Muller *et al.* (2005b) studied seasonal change in the photosynthesis–nitrogen relationship in *Aucuba japonica*, an understory shrub. The optimal

nitrogen content was higher in winter than in summer and was strongly correlated with the actual nitrogen content. It should be noted that the photosynthetic rate at the growth temperature was not constant in this study. Therefore, absolute photosynthetic rates may be regulated not to keep a certain value, but to maximize nitrogen use efficiency at the growth condition.

Conclusion

The change in temperature dependence of photosynthesis is caused by several factors. In most cases in the survey, E_{aV} increased with increasing growth temperature. Other factors, C_i , temperature dependence of J_{max} , and J_{max} to $V_{c\ max}$ ratio, were also reported to change with growth temperature, but there are interspecific differences in their responses. Among these factors, E_{aV} may be most important because photosynthesis at ambient CO_2 concentrations is generally limited by RuBP carboxylation rather than by RuBP regeneration. In particular, the shift of optimal temperature of photosynthesis is mainly explained by the change in E_{aV} . However, other factors may have substantial roles in temperature acclimation. Change in the J_{max} to $V_{c\ max}$ ratio may contribute to keeping a balance between the activities of the two processes, which may maximize nitrogen use efficiency in the photosynthetic apparatus. J_{max} often determines the temperature dependence of photosynthesis at elevated CO_2 concentrations. Incorporating changes in these parameters may contribute to better prediction of photosynthesis under a changing environment. Physiological or biochemical causes for the change in these parameters are important questions for future study.

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