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# 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 $CO_2$ concentration, activation energy of the maximum rate of RuBP (ribulose-1,5-*bis*phosphate) 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 $CO_2$ 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*., 2002*a*, *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 $CO_2$ 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 $C_3$ 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 $C_3$ photosynthesis, the photosynthetic rate is limited either by the RuBP (ribulose-1,5-*bis*phosphate) carboxylation or by the RuBP regeneration (Farquhar *et al*., 1980). The limiting step is different depending on the $CO_2$ concentration. At low $CO_2$ 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 $CO_2$ 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 $CO_2$ and $O_2$, respectively, $O$ is the $O_2$ concentration, and $\Gamma^*$ is the $CO_2$ 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 $CO_2$ 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*., 1992*a*), although use of these methods for field-grown plants is not simple. Due to a significant resistance in $CO_2$ 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 $CO_2$ conductance and thus differ from their true values (von Caemmerer *et al*., 1994). Second, for catalysis, Rubisco needs to be activated with $CO_2$ and $Mg^{2+}$. The activation state of Rubisco changes in response to light, $CO_2$ concentration, and other environmental factors (Perchorowicz *et al*., 1981; Sage *et al*., 1988; Kanechi *et al*., 1996; Feller *et al*., 1998). Regulation of activation is complex and involves the protein Rubisco activase (Salvucci and Crafts-Brandner, 2004*a*). Thus $P_c$ is affected by Rubisco kinetics, Rubisco activation state, and $CO_2$ diffusion within the leaf. In spite of the complexity, Equation 1 clearly demonstrates the $CO_2$ dependence of photosynthetic rate at low $C_i$ (von Caemmerer and Farquhar, 1981).

At high $CO_2$ 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 $CO_2$ 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 $\Delta S$ is an entropy term (Johnson *et al*., 1942; von Caemmerer, 2000; Medlyn *et al*., 2002*b*).

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 °C per 1 μmol $mol^{-1}$ $CO_2$, 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 *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*

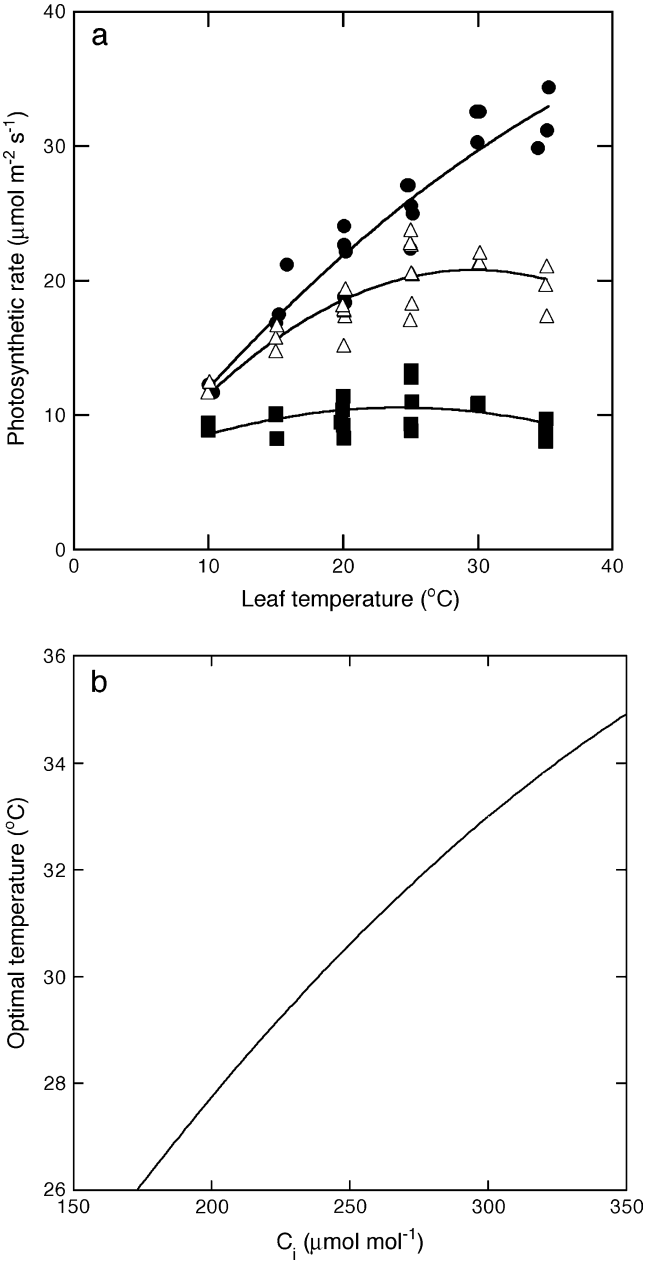


**Fig. 1.** Effect of $CO_2$ concentration on temperature dependence of photosynthesis. (a) Photosynthetic rate of *Plantago asiatica* grown at 15 °C as a function of leaf temperature. Squares, triangles, and circles denote rates determined at 200, 370, and 1000 μmol $mol^{-1}$ $CO_2$, respectively. 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).

*myrsinaefolia*; 230 and 300 μmol 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, $V_{c\,max}$ determined at a leaf-level ('apparent' $V_{c\,max}$) 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*., 2002*b*; 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 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

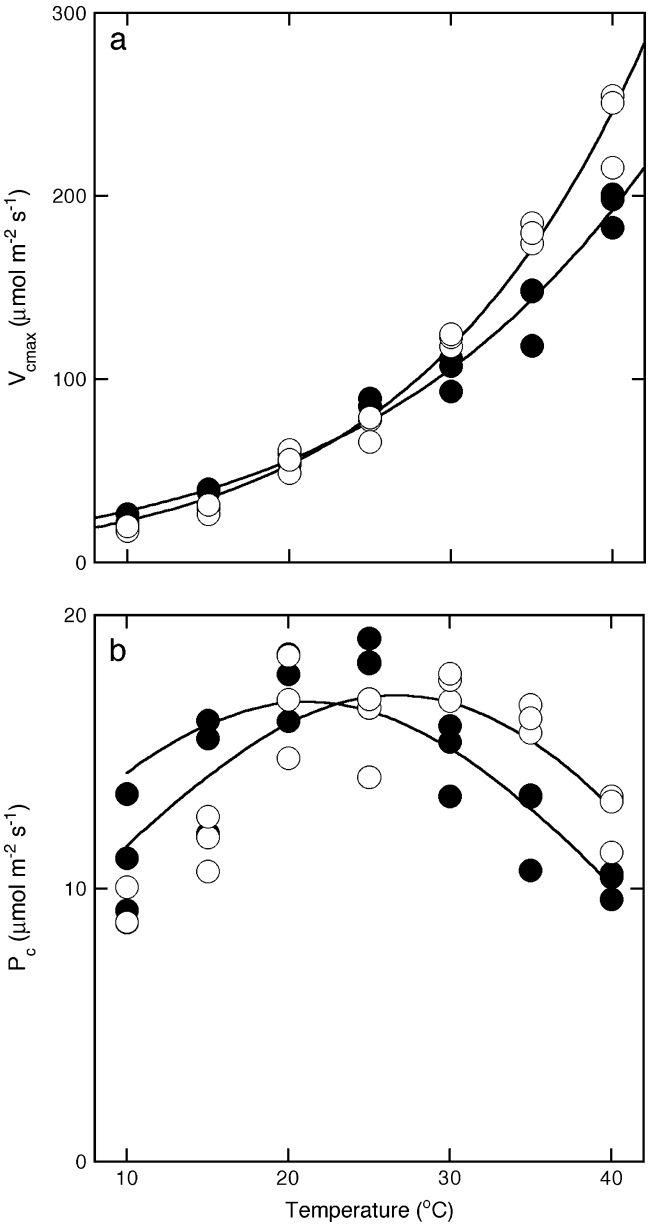


**Fig. 2.** Relationship between RuBP carboxylation-limited photosynthesis and leaf temperature. (a) $V_{cmax}$ as a function of leaf temperature. Data were obtained from *Plantago asiatica* leaves grown at 15 °C (closed circles) and 30 °C (open circles) (K Ishikawa, unpublished data) and fitted with 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 μmol 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 $C_c$.

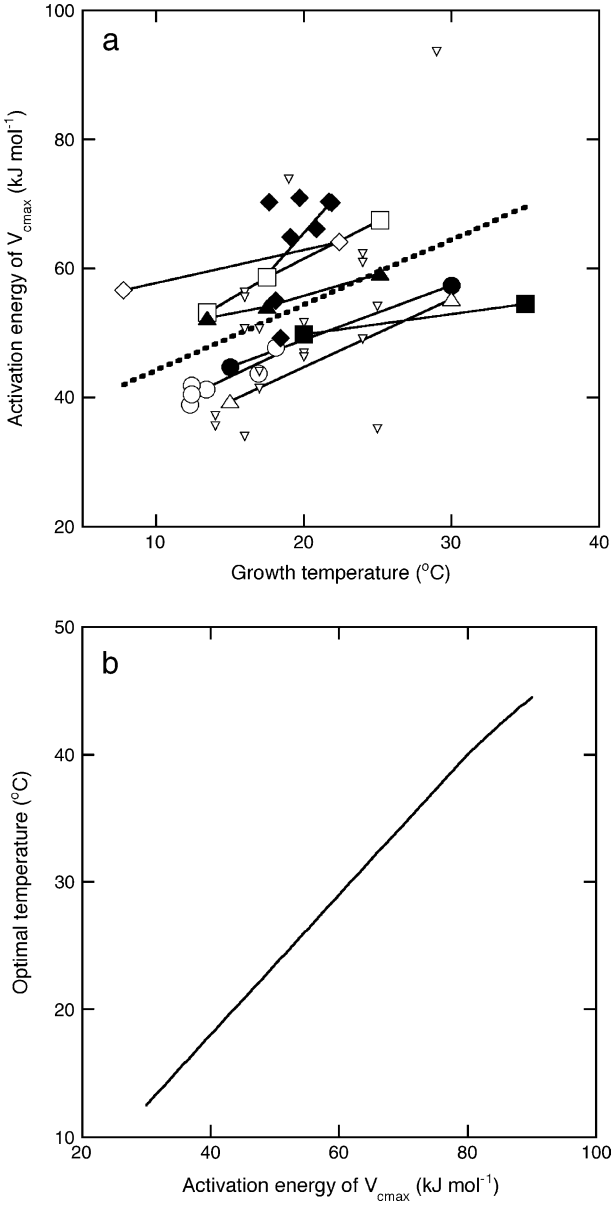


**Fig. 3.** (a) Relationship between activation energy of $V_{cmax}$ ($E_{aV}$) and growth temperature. Plants grown at controlled environment: closed circles, *Plantago asiatica* (data from K Ishikawa, unpublished results; see Fig. 2); closed squares, *Nerium oleander* (data from Hikosaka and Hirose, 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*., 2005*b*); closed triangles, potted seedlings of *Fagus crenata* (data from Onoda *et al*., 2005*b*); 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*. (2002*b*) 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+1.01$x$, $r$=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 μmol mol$^{-1}$ for $C_i$ and 65.33 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, 2004*a*). Inactivation of Rubisco at high temperature may involve a decrease in activity of Rubisco activase (Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004*a*) and an increase in the synthesis of xylulose-1,5-*bis*phosphate, the catalytic misfire product, which inactivates Rubisco (Salvucci and Crafts-Brandner, 2004*b*).

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, 2004*a*). 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 (2004*c*) 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-Brander, 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 speceis (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*., 2002*b*). 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 temperature of the Hill activity did not change (Badger *et al*., 1982). Badger *et al*. (1982) suggested that stroma FBPase (fructose-1,6-*bis*phosphatase) 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

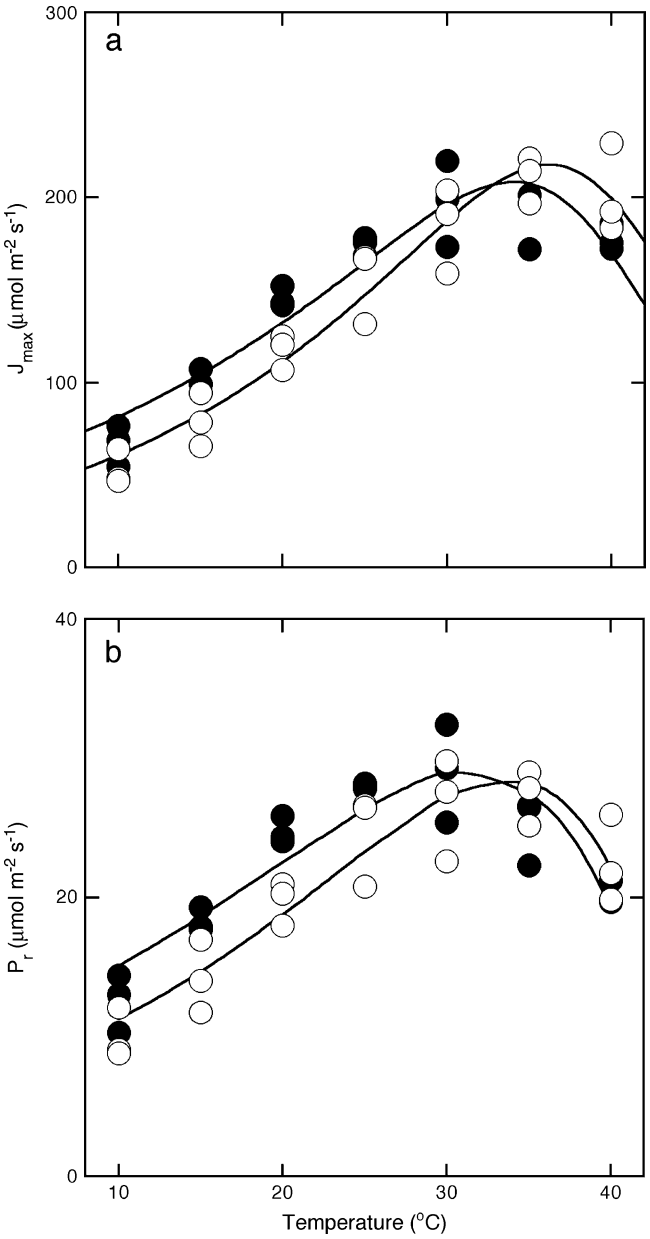


**Fig. 4.** Relationship between RuBP regeneration-limited photosynthesis and leaf temperature. Symbols are as Fig. 2. (a) $J_{max}$ as a function leaf temperature. Data points were fitted with the peak model (Equation 5) with the assumption that the energy of deactivation ($H_d$)=200 kJ mol$^{-1}$ (Medlyn *et al*., 2002*b*). Activation energy ($H_{aJ}$) was 33.8 and 42.0 kJ mol$^{-1}$ for leaves grown at at 15 °C and 30 °C, respectively. The entropy term ($\Delta S$) was 638 and 636 J K$^{-1}$ mol$^{-1}$ for leaves grown at 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.

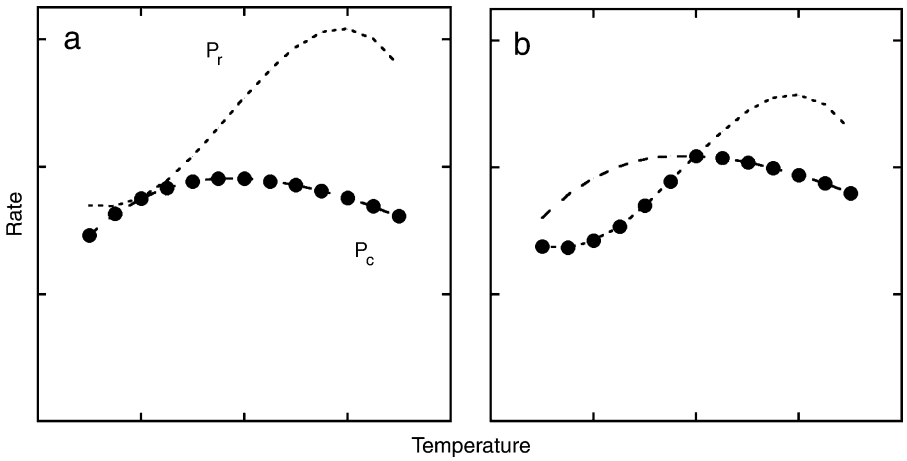


**Fig. 5.** A scheme illustrating the shift in optimal temperature of photosynthesis by the alteration in the ratio of $J_{max}$ to $V_{cmax}$. Photosynthetic rate (circles) is limited by the lower rate of $P_r$ (dotted line) and $P_c$ (broken line). $P_r$ has a higher optimal temperature than $P_c$. (a) If the $J_{max}$ to $V_{cmax}$ ratio is high, the photosynthesis–temperature curve has a low optimal temperature. (b) if the $J_{max}$ to $V_{cmax}$ 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*. (1992*b*) 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*., 2005*b*). 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 Wullschleger (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 μmol $mol^{-1}$ $CO_2$ was limited by RuBP carboxylation above 22 °C and by RuBP regeneration below 22 °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*., 2005*a*), 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*., 2002*a*), *Nerium oleander* (Hikosaka and Hirose, 2001), *Fagus crenata* (Onoda *et al*., 2005*b*), 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

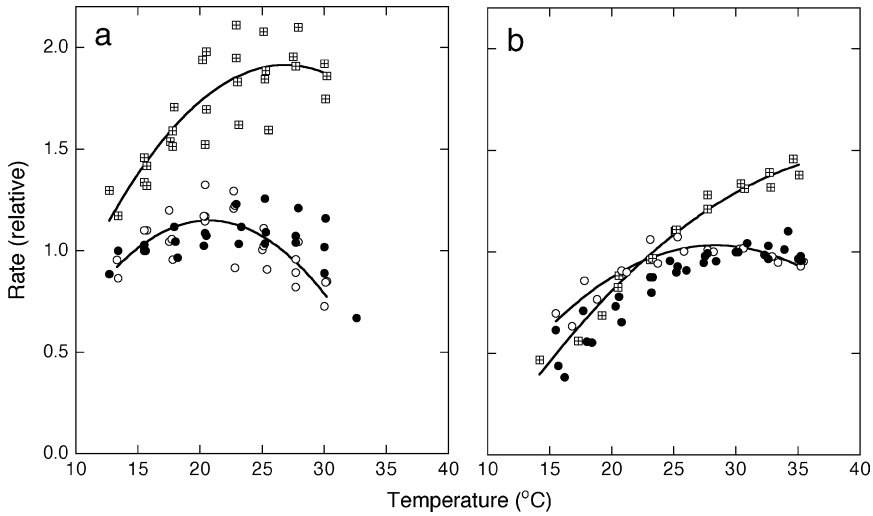


**Fig. 6.** Comparison of the photosynthetic rate and the potential rates of carboxylation ($P_c$) and regeneration ($P_r$) of RuBP at 350 μmol mol$^{-1}$ $CO_2$ for *Quercus myrsinaefolia* leaves grown at 15 °C (a) and 30 °C (b). Closed circles, measured photosynthetic rate; open circles, calculated $P_c$; 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*., 2005*b*). 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*. (2005*b*) 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 μmol 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*. (2005*a*) 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*., 2005*a*). 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*., 2005*a*). 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

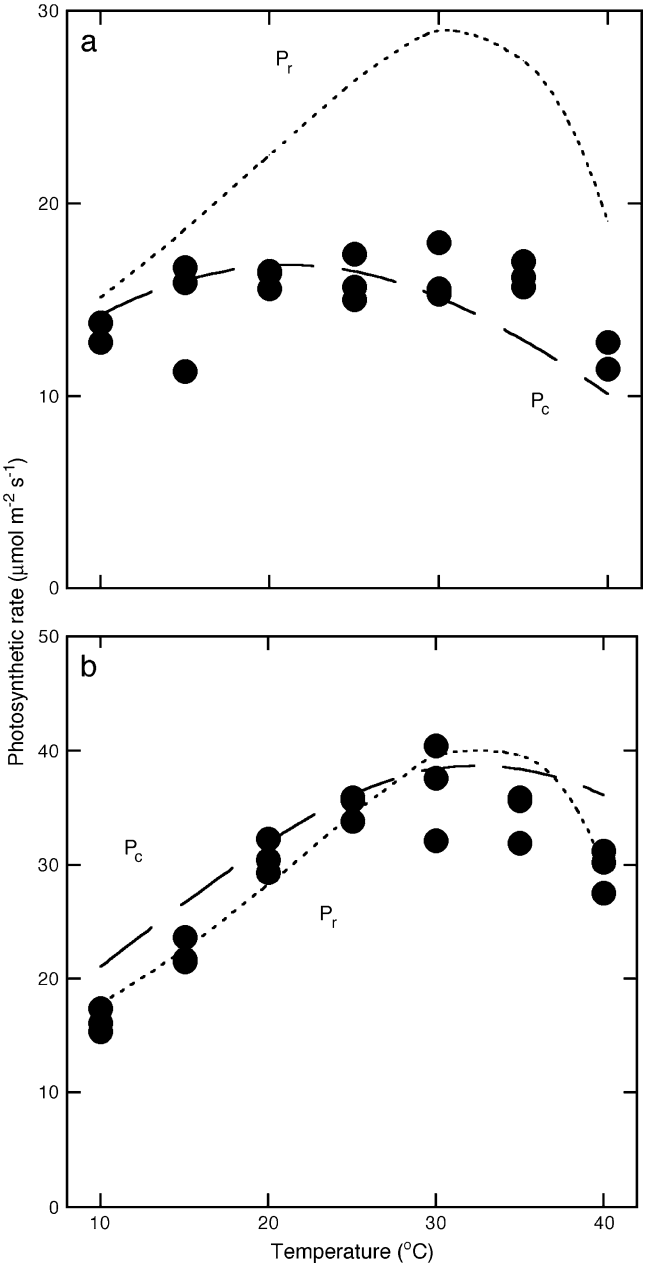


**Fig. 7.** Comparison of the photosynthetic rate and the potential rates of carboxylation ($P_c$) and regeneration ($P_r$) of RuBP at 370 (a) and 1000 μmol mol$^{-1}$ $CO_2$ (b) for *Plantago asiatica* leaves grown at 15 °C (K Ishikawa, unpublished data). Data points are measured photosynthetic rate, and lines are $P_c$ and $P_r$ calculated from temperature dependence of $V_{cmax}$ (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 $V_{c\,max}$ 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 μmol m$^{-2}$ 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*. (2005*b*) 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*. (2005*b*) studied seasonal change in the photosynthesis–nitrogen relationship in *Aucuba japonica*, an understorey 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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