Modelling Optimal Temperature Acclimation of the Photosynthetic Apparatus in C_3 Plants with Respect to Nitrogen Use

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A new hypothesis for temperature acclimation by the photosynthetic apparatus is presented. An optimization model is developed to examine effects of changes in the organization of photosynthetic components on leaf photosynthesis under various growth temperatures where the photosynthetic apparatus is not damaged. In this model, photosynthetic rate is limited either by the capacity of ribulose bisphosphate carboxylase (RuBPCase) to consume ribulose bisphosphate (RuBP), or by the capacity of RuBP regeneration. For temperature dependence of the RuBPCase activity, data from Spinacia oleracea L., which have a temperature optimum of 30 °C, are used. For temperature dependence of the capacity of RuBP regeneration, two contrasting curves that have temperature optima of 30 °C (Eucalyptus pauciflora Sieb. ex Spreng) and 40 °C (Larrea divaricata Cav.) are applied. The temperature dependence of each process is fixed for respective species, but the rate of each process varies with changes in the amounts of components. The cost of proteins, in terms of nitrogen, required to carry out each process is calculated when nitrogen is partitioned differently among photosynthetic components. The optimal nitrogen partitioning that maximizes daily photosynthesis at a given temperature is obtained. The predicted temperature optimum of the photosynthetic rate in Larrea divaricata exhibis large shifts with changes in target temperature, while shifts are negligible in Eucalyptus pauciflora. It is suggested that the shift in temperature optimum of photosynthetic rate is large when the temperature dependences of the capacities of RuBPCase and RuBP regeneration differ from each other.

Key words: Optimization model, nitrogen use efficiency, photosynthetic acclimation, temperature dependence.

INTRODUCTION

The response of photosynthesis to temperature varies not only among species but also within the same individual subjected to changing temperature regimes (Berry and Björkman, 1980). In many species, the temperature optimum of photosynthesis shifts upwards when plants are grown at higher temperatures (Lange et al., 1974; Slatyer, 1977; Mooney, Björkman and Collatz, 1978; Berry and Björkman, 1980; Badger, Björkman and Armond, 1982; Ferrar, Slatyer and Vranjic, 1989). For example, in several desert shrubs the temperature optimum can vary by more than 10 °C (Berry and Björkman, 1980). Badger et al. (1982) examined photosynthetic characteristics of such a desert shrub, Nerium oleander L. They found that, compared with leaves grown at cool temperatures, the leaves grown at high temperatures had higher photosynthetic rates at subsequent high temperatures because of increased heat stability of several photosynthetic enzymes, but they had lower rates of photosynthesis at low temperatures due to reduced enzyme activity. In their study, however, temperature dependence differed between these leaves even at temperatures where the enzymes of both leaves were stable. The temperature optimum of photosynthesis in the leaves grown at low temperature was 10 °C lower than the temperature causing thermal damage to the enzymes. This suggests that a trade-off between the amount of enzymes and their heat stability is not the only factor affecting the temperature acclimation of photosynthesis.

Farquhar, von Caemmerer and Berry (1980) modelled the instantaneous response of the photosynthetic rate to various environmental factors. In their model, the photosynthetic rate is limited either by the capacity of ribulose bisphosphate carboxylase (RuBPCase) to consume ribulose bisphosphate (RuBP) or by the capacity of RuBP regeneration. The photosynthetic apparatus is the largest sink for nitrogen in leaves (Evans and Seemann, 1989). Since nitrogen is an expensive resource for plant growth, co-limitation of the photosynthetic rate by these two capacities would be advantageous in terms of nitrogen use efficiency (Field and Mooney, 1986). Kirschbaum and Farquhar (1984) found that these capacities have different temperature dependencies. If these capacities co-limit the photosynthetic rate at a certain temperature, only one of them would limit photosynthetic rate at other temperatures with the penalty of excess investment in the other capacity. Therefore, when growth temperatures vary, changes in the organization of the photosynthetic apparatus are necessary. Farquhar and von Caemmerer (1982) suggested that the optimal ratio of the capacity of RuBPCase to that of RuBP regeneration varies depending on temperature.

Several theoretical studies have predicted that the optimal organization of the photosynthetic apparatus differs depending on growth, irradiance or CO_2 levels (Evans, 1989; HickSaka and Terashima, 1995; Medlyn, 1996). For sun and shade acclimation, the prediction was consistent...
with the actual response in plants (Evans, 1989, 1993; Hikosaka, 1996; Hikosaka and Terashima, 1996). Under shade conditions, the relative amount of chlorophyll increases to raise the photosynthetic rate at low light intensities. Similarly, the light-saturated rate of photosynthesis increases under sunny conditions. Thus, such acclimation is accompanied by changes in the response of photosynthetic rates to the target environment (Hikosaka and Terashima, 1995). A similar process may apply to the temperature acclimation of photosynthesis. In the present study, I have developed further a model of temperature acclimation of photosynthesis. In the present study, I have examined the effects of nitrogen partitioning on the temperature dependence of photosynthesis.

The temperature dependence of RuBPCase activity may be similar among various species (Badger et al., 1982; Brooks and Farquhar, 1985), while the temperature dependence of the RuBP regeneration reflects that of the electron transport at the thylakoid membrane (Kirschbaum and Farquhar, 1984). The response of electron transport to temperature differs among species (see Nolan and Smillie, 1976; Armond, Schreiber and Björkman, 1978). It is known that photosynthetic acclimation differs from species to species (Berry and Björkman, 1980; Ferrar et al., 1989). Several desert species can alter their temperature dependence of photosynthesis considerably as mentioned above, while several temperate species exhibit no, or only small changes. In the present study, two typical temperature dependencies of the RuBP regeneration rate from desert and temperate species are used to examine how the difference in the temperature dependence of each process affects optimal photosynthetic acclimation to temperature.

**THE MODEL**

The basic principle of the present model was developed in our previous studies (Hikosaka and Terashima, 1995). Photosynthetic components are categorized into five functional groups: group I, RuBPCase; group II, electron carriers, coupling factor and Calvin cycle enzymes other than RuBPCase (cyt f is used to represent this group); group III, core complex of photosystem II (PS II core); group IV, core complex of photosystem I and light harvesting chlorophyll-protein complex I (PS I); group V, light harvesting chlorophyll-protein complex II (LHC II). The capacity of RuBPCase depends on the content of group I (RuBPCase). The light-saturated rate of RuBP regeneration depends on the amount of group II and III. The photosynthetic rate at low light depends on the chlorophyll (chl) content. All the chl molecules are associated with either groups III, IV or V. Total leaf nitrogen content is fixed and allocation of nitrogen to each group can be altered. The optimal nitrogen partitioning among photosynthetic components which maximizes daily photosynthesis in a given environment is calculated.

**Photosynthetic rate**

Instantaneous responses of photosynthesis to environmental factors are modelled according to Farquhar et al. (1980) with some modifications. The photosynthetic rate ($P$) is given by a minimum of the RuBP-saturated rate of photosynthesis ($P_e$) and the RuBP-limited rate of photosynthesis ($P_l$):

$$P = \min\{P_e, P_l\}.$$  

$P_l$ is expressed as:

$$P_l = \frac{V_{\text{max}}(p - \Gamma^*)}{p_c + K_p(1 + O/K_o)} - R,$$  

where $R$ is the dark respiration rate, $V_{\text{max}}$ is the maximum velocity of RuBP carboxylation per leaf area, $p_c$ is the CO$_2$ level at chloroplasts in terms of the partial pressure, $K_p$ and $K_o$ are the Michaelis constants for CO$_2$ and O$_2$, respectively and $O$ is the partial pressure of O$_2$. (See Appendix for abbreviations and units.) $\Gamma^*$ is the CO$_2$ compensation point in the absence of respiration defined as follows:

$$\Gamma^* = \frac{0.5V_{\text{max}}K_pO}{V_{\text{max}}},$$  

where $V_{\text{max}}$ is the maximum velocity of RuBP oxygenation per leaf area. $P_e$ is expressed as follows:

$$P_e = \frac{J_p(p - \Gamma^*)}{4p_c + 8\Gamma^*} - R,$$  

where $J$ is the rate of electron transport on a leaf area basis. $J$ is expressed as,

$$J = \frac{\phi_s I + J_{\text{max}} - (\phi_s I + J_{\text{max}})^2 - 4\phi_s I\theta J_{\text{max}}^{3/2}}{2\theta},$$  

where $I$ is the incident photon flux density (PFD), $J_{\text{max}}$ is the light-saturated rate of $J$, $\phi_s$ is the initial slope of the curve and $\theta$ is the convexity of the curve. In the present study, the Blackman-type response of $J$ to $I$ is assumed ($\theta \rightarrow 1$).

The partial pressure of intercellular CO$_2$ ($p_c$) is assumed to be a constant fraction of that of atmospheric CO$_2$ ($p_a$),

$$p_c = cp_a,$$  

(Sage, 1994). Then, $p_a$ is given as,

$$p_a = p_c - P/g_a,$$  

where $g_a$ is the conductance for CO$_2$ from the intercellular space to the chloroplasts, which is assumed to be a function of the RuBPCase content (see Evans et al., 1994),

$$g_{a_{25}} = a_1[\text{RuBPCase}] + b_1,$$  

where the suffix 25 means temperature at 25 °C, $a$ and $b$ are constants (see Table 1) and components in the square brackets represent their amounts on a leaf area basis.

Parameters for the photosynthetic rate are expressed as a function of the amount of each group:

$$V_{\text{max}} = k_{\text{cat}}[\text{RuBPCase}],$$  

$$J_{\text{max}} = a_{\text{cat}[cyl]} = a_{\text{cat}[\text{PS II}]},$$  

$$\phi_s = a_{\text{chl}}/[b_s + \text{chl}],$$  

where $k_{\text{cat}}$ is the specific activity of RuBPCase. Equation (9) means that the RuBP-saturated rate of photosynthesis depends on the amount of RuBPCase and eqn (10) means
that the RuBP-limited rate of photosynthesis under saturated light depends on the amount of group II and III (see von Caemmerer and Farquhar, 1981). Equation (11) indicates that the initial slope of the light-response curve of photosynthesis depends on the chl content (Gabrielsen, 1948).

The amount of PS I is assumed to be parallel to that of the chl content:

$$[\text{PS I}] = a_{\text{chl}}$$

(see Hikosaka and Terashima, 1995, 1996). The amount of LHC II is estimated on the assumption that every chl molecule is bound either to the PS II core, to PS I, or to LHC II; thus,

$$[\text{LHC II}] = (1000[\text{chl}] - \text{chl}_{\text{PS I}}[\text{PS I}] - \text{chl}_{\text{PS I}}[\text{PS I}]) / \text{chl}_{\text{LHC II}}$$

(13)

where chl\_x denotes the number of chl molecules associated with chl-protein complex X, and 1000 is an adjustment factor for differences in the units (see Hikosaka and Terashima, 1995).

Nitrogen costs (nitrogen molecules in each group) of the photosynthetic components are calculated according to Hikosaka and Terashima (1995). Photosynthetic nitrogen, $N_p$, is the sum of nitrogen in all the components:

$$[N_p] = n_{\text{RuBPCase}} + n_{\text{PS II}}[\text{PS II}] + n_{\text{PS I}}[\text{PS I}] + n_{\text{LHC II}}[\text{LHC II}]$$

(14)

where $n_x$ is the nitrogen cost of group x.

Since $[\text{PS I}]$ is a function of [chl] [eqn (12)], [LHC II] is a function of [PS II] and [chl]. By substituting eqns (10), (12) and (13) into (14) with appropriate rearrangements, [RuBPCase] is expressed as a function of $[N_p]$, [PS II] and [chl]. Therefore, the amount of each group is expressed as a function of $[N_p]$, [PS II] and [chl]. The leaf nitrogen content, [N], is expressed as a function of $[N_p]$ (Hikosaka and Terashima, 1995),

$$[N] = a_{1}[N_p] + b_a$$

(15)

The respiration rate at 25 °C ($R_{25}$) is expressed as a function of [N],

$$R_{25} = a_{2}[N] + b_a$$

(16)

(Hirose and Werger, 1987; see Hikosaka and Terashima, 1995).

The daily change of PFD is assumed to follow a square sine curve,

$$I = I_0 \sin^2(\pi(t - 6)/12) \quad (6 \leq t < 18)$$

$$I = 0 \quad (0 \leq t < 6, 18 \leq t < 24),$$

(17)

where $t$ is the solar time and $I_0$ is the PFD at noon ($t = 12$).

Daily photosynthesis, $P_{\text{day}}$, is expressed as an integration of $P$ throughout the day,

$$P_{\text{day}} = \int_0^{24} P \, dt.$$  

(18)

**Temperature dependence**

In the present study, the temperature dependence of each parameter is incorporated on the assumption that values at 25 °C are the same as those previously assumed (Hikosaka and Terashima, 1995, see Table 1).

Temperature dependence of the respiration rate follows Lloyd and Taylor (1994):

$$R = R_{25} \exp \{E_a/298.2/R(1 - (298.2/T))\}$$

(19)

where $R$ is the universal gas constant, $T$ is the absolute temperature (K) and $E_a$ is the activation energy.

The main limiting step for CO$_2$ diffusion from the intercellular space to chloroplasts may be water in the cell wall (Evans et al., 1994; Terashima et al., 1995a).

Temperature dependence of the diffusion coefficient of CO$_2$ in water (Hesketh et al., 1983) is applied for the calculation of $g_a$:

$$g_a = g_{a25} - 6.81 + 0.0426T.$$  

(20)

The temperature dependence of kinetic parameters of RuBPCase is assumed to be similar among C$_3$ species (Badger et al., 1982; Brooks and Farquhar, 1985). The temperature dependencies of $V_{\text{cmax}}$, $V_{\text{max}}$, $K_c$ and $K_t$ determined by Jordan and Ogren (1984) for *Spinacia oleracea in vitro* are fitted by a polynomial (the temperature

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**Table 1. Constants used in the model**

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<th>Parameter</th>
<th>Unit</th>
<th>Value</th>
<th>Equation</th>
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See Appendix for abbreviations.
* See text.
† von Caemmerer et al., 1995.
‡ Evans et al., 1994.
* Terashima and Evans, 1988. $J_{\text{max}}$ is assumed to be 44 fold (1.1 x 4) the rate of O$_2$ evolution at 1800 $\mu$ mol quanta m$^{-2}$ s$^{-1}$ and saturated CO$_2$.
dependence of each parameter is shown in Terashima et al., 1995b):

\[
V_{\text{max}} = V_{\text{max}25} \times (-615.85 + 6.78T - 0.0249474T^2 + 3.0677 \times 10^{-5}T^3),
\]

(21)

\[
V_{\text{max}} = V_{\text{max}25}(-9.94 + 0.0367T),
\]

(22)

\[
K_v = K_{v25}(-1654.72 + 17.748T - 0.063526T^2 + 7.5884 \times 10^{-5}T^3),
\]

(23)

\[
K_s = K_{s25}(-4.05 + 0.0169T).
\]

(24)

Thus, we obtained the temperature dependence of \( P_l \) as shown in Fig. 1.

Two contrasting types of the temperature dependence of \( J_{\text{max}} \) are used in the present study. One is obtained from leaves of a temperate evergreen wood, *Eucalyptus pauciflora*, determined by Kirschbaum and Farquhar (1984) using the gas exchange method:

\[
J_{\text{max}} = J_{\text{max}25}(1 + 0.0409(T - 298.2^\circ) - 0.00154)
\times (T - 298.2)^2 - 9.42 \times 10^{-5}(T - 298.2)^3.
\]

(25)

The other is temperature dependence of the Hill activity of a desert shrub, *Larrea divaricata*, grown at 45 °C (Armond et al., 1978):

\[
J_{\text{max}} = J_{\text{max}25}(1 + 0.066146(T - 298.2) + 0.0031189(T - 298.2)^2 - 7.139 \times 10^{-5}(T - 298.2)^3 - 5.1282 \times 10^{-9}(T - 298.2)^4).
\]

(26)

The temperature dependence of \( J_{\text{max}} \) is fixed in each species. The temperature dependence curves of \( P_l \) under saturated light have optima which differ between the two species (Fig. 1).

As mentioned above, the amount of each component can be expressed as a function of three variables, [N], [chl] and [PS II]. Therefore, combining all the equations, we can calculate \( P_{\text{sat}} \) from \( T, I_o, P_o, [N], [\text{chl}] \) and [PS II]. \( P_o \) is fixed to be 35 Pa in the present study. The optimal combination of [chl] and [PS I] that maximizes \( P_{\text{sat}} \) at given [N], T and \( I_o \) is calculated numerically.

### RESULTS

#### Shift of temperature optima of photosynthesis

Figure 2 shows temperature dependencies of the instantaneous photosynthetic rate (\( P \)) at \( I = 2000 \mu \text{mol m}^{-2} \text{s}^{-1} \) (Fig. 2A and B) and of daily photosynthesis (Fig. 2C and D) of leaves optimized at 10, 20, 30 and 40 °C and at \( I_o = 2000 \mu \text{mol m}^{-2} \text{s}^{-1} \). It is assumed that there are no changes in leaf temperature throughout the day. The nitrogen content is fixed at 0.18 mol m\(^{-2}\). A decrease in the daily rate at high temperatures in both species results from an increase in the respiration rate with increasing temperature [eqn (19)]. In *E. pauciflora*, differences in the temperature dependence of \( P \) in the leaves optimized at different temperatures are small. On the other hand, in *L. divaricata*, the temperature optima clearly shift towards the temperature at which leaf photosynthesis is optimized. The temperature maximizing daily photosynthesis is identical to the optimized temperature in leaves for 20 and 30 °C, but not for 40 °C.

Differences in the temperature dependence of \( P \) among leaves which have different optimal temperatures for photosynthesis are due to the difference in the processes limiting \( P \). For example, in *L. divaricata*, \( P \) of the 20 °C leaf is limited by \( P_o \) at every temperature, while \( P \) of the 40 °C leaf is limited by \( P \) at every temperature. However, \( P \) at the target temperature where leaf photosynthesis is optimized is co-limited both by \( P_o \) and \( P \) in each leaf. In the 30 °C leaf \( P \) is limited by \( P \) below 30 °C, but by \( P_o \) above 30 °C (see also Fig. 1 for temperature dependences of \( P_o \) and \( P \)).

#### Nitrogen partitioning

The optimal contents of three representative components under various temperature conditions at \( I_o = 2000 \mu \text{mol m}^{-2} \text{s}^{-1} \) are compared (Fig. 3). The nitrogen content is fixed at 0.18 mol m\(^{-2}\). In both species, the chl content increases with increasing temperature, which partly compensates for the decrease in the quantum yield of photosynthesis with increasing temperature (Ehleringer and Björkman, 1977; Farquhar et al., 1980). In *E. pauciflora*, changes in both contents of RuBPCase and cyt f are small except at 40 °C. On the other hand, in *L. divaricata*, the RuBPCase content increases with increasing temperature while the cyt f content decreases except at 15 °C. Since the RuBP-limited rate of photosynthesis increases with increasing temperature in *L. divaricata* (Fig. 1), an increase of the RuBPCase content with increasing temperature is necessary.

#### Effects of daily temperature changes

The effects of daily temperature changes on photosynthesis were examined. Four types of temperature change...
are studied (Fig. 4), with average daytime temperatures being identical, while the fluctuations in a day are different. There is no fluctuation in type I, whereas in type IV the difference between the maximum and the minimum temperatures is 24 °C. Figure 5 shows daily photosynthesis at temperatures with different averages and daytime fluctuations. The nitrogen partitioning among photosynthetic components is optimized under each temperature condition. To avoid effects of respiration at night, only net photosynthesis during daytime (6 ≤ t < 18) is calculated. Except for E. pauciflora at an average temperature of 35 °C, daily photosynthesis increases with an increase in the temperature difference in daytime. Two factors are involved in this response. One is the temperature response to the initial slope of the light-response curve. As mentioned above, the quantum yield increases with decreasing temperature. Thus, low temperatures at the beginning and the end of the day are beneficial for daily photosynthesis. The other is the temperature dependence of $J_{\text{max}}$. Since the optimal temperature of $J_{\text{max}}$ is higher than the average temperatures in L. diwaricata, the increase in the temperature at noon increases the photosynthetic rate. This is also the case in E. pauciflora at average temperatures of 15 and 25 °C. However, in E. pauciflora at the average temperature of 35 °C, the increase in temperature at noon does not increase photosynthesis because $J_{\text{max}}$ decreases with temperatures above 35 °C. Because of these factors, trends in the change of the optimal partitioning with the daily temperature pattern are different depending on species and on mean temperatures. However, effects of change in the daily temperature pattern on the optimal partitioning are small (data not shown), except for E. pauciflora at the average temperature of 25 °C: the RuBPCase content in type IV was 10% lower than that in type I.

**DISCUSSION**

**Optimal acclimation to temperature**

The present study shows that changes in nitrogen partitioning among photosynthetic components can be a factor responsible for the shift in the optimal temperature for photosynthesis. Figure 6 shows a scheme illustrating the shift in the temperature optimum of photosynthesis. The photosynthetic rate (solid line) is limited by the lower rate of two processes, which both have different temperature dependencies. If the investment of nitrogen in the process that has a lower optimal temperature (α) is reduced and
that in the other ($\beta$) is increased, $P$ has a lower optimal temperature (Fig. 6A). Conversely, if investment in $\alpha$ is increased, the temperature optimum of $P$ shifts from low (broken line) to high (Fig. 6B). Therefore, this shift occurs when the temperature dependence of the two limiting processes, $P_{s}$ and $P_{l}$, are different. In Larrea ditericata, whose $P_{s}$ has a temperature optimum higher than that of $P_{l}$, the temperature dependence of $P$ changes strongly with changes in the nitrogen partitioning (Fig. 2B and D). When nitrogen is partitioned to maximize daily photosynthesis, $P_{s}$
Fig. 7. Photosynthetic acclimation in a desert shrub, Nerium oleander. Data were obtained from N. oleander leaves grown at 20 °C (○) and 45 °C (●), respectively (replotted from Badger et al., 1982). Solid and dotted lines are simulated photosynthetic rate of leaves of L. divaricata optimized at 20 and 45 °C, respectively. For temperature dependence of $I_{\text{max}}$, eqn (25) is used. The leaf nitrogen content is adjusted for fitting. For leaves optimized at 20 and 45 °C, $[\text{N}]$ is 0.102 and 0.092 mol m$^{-2}$, respectively. Content of chl (mmol m$^{-2}$), RuBPCase (µmol m$^{-2}$) and cyt $f$ (µmol m$^{-2}$) is 0.11, 3.13 and 0.95 in the 20 °C leaf and 0.11, 3.20 and 0.55 in the 45 °C leaf.

and $P$ co-limit $P$ at $I = I_{\text{a}}$ under growth temperature conditions.

Figure 7 shows the temperature acclimation of Nerium oleander redrawn from Badger et al. (1982). Nerium oleander exhibits a temperature response quite similar to that of L. divaricata (see Berry and Björkman, 1980). As mentioned previously, the temperature dependence of $P$ was different between leaves grown at contrasting temperatures, even below 35 °C, where enzymes of both leaves may be stable (Badger et al., 1982). Stability of enzymes is also suggested by the fact that the temperature dependencies of the photosynthetic rate at saturated CO$_2$ were similar between these leaves below 35 °C (Badger et al., 1982). The simulation results of the present model are compared with actual data (Fig. 7; note that only nitrogen content is adjusted to fit the actual data). The simulation results explain the difference in the temperature dependence of $P$ well. Between 20 and 35 °C, $P$ of leaves grown at lower temperatures is limited by RuBPCase, while $P$ of leaves grown at higher temperatures is limited by the RuBP regeneration.

In Eucalyptus pauciflora, the temperature optimum of $P_s$ is relatively similar to that of $P_s$ (Fig. 1). Therefore, effects of nitrogen partitioning on the temperature dependence of $P_s$ are minor and the difference in optimal nitrogen partitioning is small at different temperatures (Figs 2A, C and 3). It should be noted that the shift of the temperature optimum of $P_s$ occurs only between the temperature optima of the two limiting processes. Adjustment of the temperature optimum of photosynthesis to the growth temperature is not always possible. When one species exhibits little change in photosynthetic performance in spite of changes in growth temperature, two explanations exist: either it does not have the ability to acclimate, or the optimal nitrogen partitioning is independent of growth temperature because temperature dependencies of $P_s$ and $P$ are similar.

Although the photosynthesis-temperature curve predicted by the present study does not show the shift in the temperature optima in E. pauciflora (Fig. 2A), it is known that the temperature optima of E. pauciflora leaves actually shift with growth temperatures (Slatyer, 1977; Ferrar et al., 1989). This difference may be due to the temperature dependence of $P_s$. Kirschbaum and Farquhar (1984) showed that the apparent activation energy of $V_{\text{max}}$ of E. pauciflora determined from gas exchange was slightly lower than that of $V_{\text{max}}$ of Spinacia oleracea determined by Jordan and Ogren (1984), which is used in the present study (unfortunately, the temperature dependence of $V_{\text{max}}$ shown in Kirschbaum and Farquhar could not be used because they did not show the temperature dependence of $K_s$, $K_c$ and $V_{\text{max}}$ used for the calculation of $V_{\text{max}}$). Therefore, the temperature optimum of $P_s$ in E. pauciflora would be slightly lower than that of $P_s$ predicted by the present model and would be slightly lower than that of $P_s$. This may allow a small shift of the temperature optimum of $P_s$ in E. pauciflora. It should be noted, however, that the actual shift in optimum temperature for $P_s$ in E. pauciflora was only 5 °C (Slatyer, 1977), which was smaller than that of other Eucalyptus species and was much smaller than that of desert shrubs (Ferrar et al., 1989).

In the present study, only the temperature dependence of RuBP regeneration is assumed to be inherently different among species. Although there seems to have been relatively little comparative study on the specific variation in temperature dependence of RuBP regeneration, a survey of the literature suggests that the optimum temperature of the electron transport rate of hot desert species is much higher than that of temperate species (Armond et al., 1978; Badger et al., 1982). On the other hand, the difference in the temperature dependence of the kinetic parameters of RuBPCase may be minor between temperate and desert species (Badger et al., 1982). If this is true, the potential for changing the temperature optimum of $P_s$ is higher in species living in hot habitats. This idea is consistent with the fact that, among Eucalyptus species investigated by Ferrar et al. (1989), E. pauciflora is distributed in the coldest region.

Recently, Makino, Nakano and Mae (1994), and Sage, Santrucek and Grise (1995) examined effects of growth temperature on photosynthetic acclimation in Oryza sativa and Chenopodium album, respectively. In both species, the chl content was higher in leaves grown under higher temperature, which is consistent with the present prediction (Fig. 3). The amounts of RuBPCase and parameters related to the electron transport were less sensitive to growth temperature. This may also be consistent with results here if the optimal temperature of $P_s$ in these species is similar to that of E. pauciflora. In fact, the optimal temperature of the electron transport rate in C. album was 30–35 °C (Sage et al., 1995), which is close to that of $P_s$ in E. pauciflora (Fig. 1). It is also possible that these annual plants do not have the ability to acclimate to various temperatures, because seasonal change in growth temperature may be small for
annuals relative to evergreen species (Berry and Björkman, 1980).

Assumptions

In the present study, temperature dependencies of $P_c$ and $P_r$ are assumed to be insensitive to growth temperature. However, Badger et al. (1982) showed that the heat stability of several enzymes in *N. oleander* leaves changes depending on growth temperature. Studies on several temperate species suggest that $V_{\text{max}}$ determined *in vitro* using the gas exchange method at higher temperature ($> 35^\circ \text{C}$) is lower than $V_{\text{max}}$ determined *in vitro* (Kirschbaum and Farquhar, 1984; Harley and Tenhunen, 1991). Therefore, the predicted photosynthetic rate of low temperature-grown leaves at higher temperatures may be higher than the actual rate. For example, in Fig. 7, the decrease in the predicted $P$ with increasing temperature in the leaf grown at low temperature was less steep than the actual data. However, the temperatures effecting thermal damage of enzymes are much higher than the growth temperature ($> 15^\circ \text{C}$ in *Nerium oleander*, Badger et al., 1982).

It is known that the temperature dependence of the electron transport rate changes with growth temperature (Armond et al., 1978; Badger et al., 1982; Mitchell and Barber, 1986). Badger et al. (1982) and Mitchell and Barber (1986) showed that the electron transport rate on a chl basis at low temperature was higher in low temperature-grown plants. However, since LHC II is not directly related to the electron transport, the electron transport rate on a chl basis is not a good index for nitrogen use efficiency of electron transport. Thus, the extent of improvement in the electron transport per unit of related nitrogen is still unclear. In fact, there was no advantageous change in *L. divaricata* when the electron transport rate was expressed on a chl basis (Armond et al., 1978). Although quantitative prediction is difficult, the possible effects of temperature acclimation on electron transport can be summarized as follows: if the improvement in the electron transport rate per unit of related nitrogen is considerable, the optimal investment of nitrogen into group II and III at lower temperatures is lower than the present prediction. Generally, apparent activation energy of the electron transport rate decreases with decreasing growth temperature (Mitchell and Barber, 1986). This affects the shape of temperature dependence of the photosynthetic rate. However, since the temperature optimum of the electron transport rate is insensitive to growth temperature (Armond et al., 1978; Badger et al., 1982), the range within which the temperature optimum of the photosynthetic rate can change is not affected by the acclimation in the electron transport.

The limitation to photosynthesis due to triose phosphate utilization (TPU; Sharkey, 1985) is ignored in the present study. Labate and Leegood (1988) showed that, in barley grown at 30 °C, TPU limits $P$ below 15 °C. The activation energy of the TPU limited rate of photosynthesis is higher than that of photosynthesis limited by other processes (Labate and Leegood, 1988). However, information about TPU limitation is very restricted. In particular, a lack of knowledge of its linkage with leaf nitrogen and temperature dependence at higher temperatures makes modelling difficult (Harley and Tenhunen, 1991; Medlyn, 1996). TPU limitation is not commonly observed when photosynthetic rates are measured under the growth condition (Socias, Medrano and Sharkey, 1993) except for the case of low sink strength (Stitt, 1991). Therefore, the effect of ignoring TPU limitation may be negligible at higher temperatures. On the other hand, because of the higher activation energy, TPU limitation may occur at lower temperatures. If TPU limits $P$ at lower temperatures, the actual decrease in $P$ with decreasing temperature would be steeper than that predicted. In Fig. 7, such a tendency can be seen in the leaf grown at high temperature.

In the present study, the CO$_2$ partial pressure in the intercellular space is assumed to be a constant fraction of that in air, independent of temperature. This assumption is valid only when the water vapour deficit is constant (Leuning, 1995). Under low air humidity or water stress, stomata close to prevent water loss and to maintain constant water use efficiency (Cowan, 1977) and thus the intercellular CO$_2$ level changes. The temperature optima of $P$ change with CO$_2$ level (Berry and Björkman, 1980; Farquhar et al., 1980). Kirschbaum and Farquhar (1984) showed theoretically that the shift in temperature optima can be explained by the control of stomata without any changes in the photosynthetic apparatus. However, higher leaf temperature generally accompanies an increase in the water vapour deficit, especially in a desert. Since stomatal closure results in a shift in the temperature optima of photosynthesis to lower temperatures (Kirschbaum and Farquhar, 1984), stomatal regulation may not positively contribute to the shift in the temperature optima of the photosynthetic rate.

CONCLUSIONS

Previous studies have concluded that the trade-off relationship between the amount and thermal stability of photosynthetic enzymes is a factor responsible for the temperature acclimation of photosynthesis (Berry and Björkman, 1980; Badger et al., 1982; Ferrar et al., 1989). The present study suggests that the change in nitrogen partitioning among the photosynthetic components could be another factor. It is also suggested that, under temperatures at which the enzymes are stable, the shift in the optimum temperature of photosynthesis is possible only when the temperature dependencies of activities of photosynthetic components are different. In other words, flexibility in the temperature dependence of the photosynthetic rate depends on the temperature dependence of each process of photosynthesis. Therefore, not all species can exhibit apparently advantageous acclimation to various temperatures.

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LITERATURE CITED


APPENDIX
Abbreviations and units (see also Table 1)

CF, Coupling factor
chl, Chlorophyll
[chl], Leaf chl content (mmol m\(^{-2}\))
[chl\(_x\)], Number of chl molecules associated with chl-complex x
cyt\(_f\), Cytochrome \(_f\)
[cyt\(_f\)], Leaf cyt\(_f\) content (\(\mu\) mol m\(^{-2}\))
\(E_a\), Activation energy of respiration (J mol\(^{-1}\))
\(g_{av}\), Conductance of CO\(_2\) from intercellular space to chloroplast (\(\mu\) mol m\(^{-2}\) s\(^{-1}\) Pa\(^{-1}\))
\(I\), Incident photon flux density (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))
\(J\), Rate of electron transport (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))
\(J_{\text{max}}\), Light saturated rate of electron transport (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))
\(k_{\text{cat}}\), Specific activity of RuBPCase (mol mol\(^{-1}\) protein s\(^{-1}\))
\(K_c, K_o\), Michaelis constants for CO\(_2\) and O\(_2\) respectively (Pa, kPa)
LHC, Light harvesting chl-protein complex
[LHC II], leaf LHC II content (\(\mu\) mol m\(^{-2}\))
[N], Leaf nitrogen content (mol m\(^{-2}\))
\(N_{\text{p}}\), Nitrogen in photosynthetic components
\([N]_{\text{p}}\), Leaf photosynthetic nitrogen content (mol m\(^{-2}\))
n_{\text{x}}, Nitrogen cost of group x (mol mol\(^{-1}\))
\(O\), Partial pressure of O\(_2\) (kPa)
P, Instantaneous rate of photosynthesis (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))
\(p_c\), Partial pressure of atmospheric CO\(_2\) (Pa)
\(p_{o_{\text{c}}}\), CO\(_2\) level at chloroplast in terms of partial pressure (Pa)
P\(_{\text{day}}\), Daily rate of photosynthesis (mol m\(^{-2}\) d\(^{-1}\))
PFD, Photon flux density
\(p_{c}\), Partial pressure of intercellular CO\(_2\) (Pa)
\(P\), RuBP-limited rate of photosynthesis (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))
\(P_{\text{r}}\), RuBP-saturated rate of photosynthesis (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))

\(PS\ I\), Core complex of photosystem I and LHC I

[PS I], Leaf PS I content (\(\mu\) mol m\(^2\))
PS II core, Core complex of photosystem II

[PS II], Leaf PS II content (\(\mu\) mol m\(^2\))
\(R\), Rate of dark respiration (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))
\(R\), Universal gas constant (J mol\(^{-1}\) K\(^{-1}\))

RuBP, Ribulose-1,5-bisphosphate

RuBPCase, Ribulose-1,5-bisphosphate carboxylase

[RuBPCase], Leaf RuBPCase content (\(\mu\) mol m\(^2\))

\(t\), Time of day (h)

\(T\), Absolute temperature (K)

\(v_{\text{max}}\), Maximum velocity of RuBP carboxylation (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))

\(v_{\text{max}}^r\), Maximum velocity of RuBP oxygenation (\(\mu\) mol m\(^{-2}\) s\(^{-1}\))

\(\Gamma^*\), CO\(_2\) compensation point in the absence of dark respiration (Pa)

\(\phi\), Initial slope of light response curve of RuBP regeneration rate (mol mol\(^{-1}\))

\(\theta\), The convexity of light response curve of RuBP regeneration rate (no dimension)

Values with a subscript of ‘25’ mean the value at 25 °C.