Leaf and canopy photosynthesis of C₃ plants at elevated CO₂ in relation to optimal partitioning of nitrogen among photosynthetic components: theoretical prediction

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Abstract

Effects of changes in the organization of photosynthetic components on leaf photosynthesis under contrasting atmospheric CO₂ conditions (35 and 70 Pa) are evaluated using an optimization model, in which 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 nitrogen cost of photosynthetic components to carry out each process is calculated for the optimal partitioning of nitrogen among the components. The model predicts that nitrogen allocation to the components carrying out RuBP regeneration should be increased with reduction in allocation to RuBPCase to maximize daily photosynthesis at 70 Pa CO₂. At a temperature of 25°C, doubling the current CO₂ level increases daily photosynthesis by 60% with optimal reallocation of the nitrogen partitioning while the increase without reallocation of nitrogen is 40%. However, at lower growth irradiance, the advantage in daily photosynthesis due to the reallocation decreases with increasing nitrogen content. The ratio of photosynthesis at 70 Pa to that at 35 Pa increases with increasing temperature. The effects of CO₂ levels on photosynthesis of a canopy in which nitrogen is optimally allocated among leaf layers are also examined. At 25°C, canopy photosynthesis at the doubled CO₂ level is predicted to increase 60 and 40% with and without the optimization of nitrogen partitioning among photosynthetic components, respectively. Doubling the CO₂ level does not affect the optimal nitrogen distribution among leaf layers in the canopy irrespective of optimization of nitrogen partitioning among photosynthetic components. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: CO₂ elevation; Canopy photosynthesis; Global change; Model; Photosynthetic acclimation; Photosynthetic apparatus; Nitrogen partitioning

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1. Introduction

Because CO₂ is a primary substrate of photosynthesis, the photosynthetic rate increases with increasing CO₂ concentrations in C₃ plants. Its biochemical basis was theoretically clarified by Farquhar et al. (1980). 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. At low CO₂ concentrations, the capacity of RuBPCase limits photosynthesis, while the capacity of RuBP regeneration does so at high CO₂ concentrations. These two processes are considered to co-limit photosynthesis at the current concentration of CO₂ (Wullschleger, 1993). Therefore, photosynthesis may be limited by the RuBP regeneration process under high atmospheric CO₂ conditions (or possibly by inorganic phosphate regeneration (Sharkey, 1985)).

However, if the balance between capacities of RuBP regeneration and RuBPCase does not change at high CO₂ concentrations, the capacity of RuBPCase does not limit photosynthesis and part of the investment in RuBPCase may be wasted. Several researchers have indicated that photosynthetic acclimation, i.e. changes in nitrogen partitioning among photosynthetic components, can improve the photosynthetic rate at high CO₂ concentrations (Hogan et al., 1991; Sage, 1994; Webber et al., 1994). When the amount of RuBPCase is reduced to reallocate nitrogen to proteins which carry out RuBP regeneration, these proteins may co-limit photosynthesis at high CO₂ concentrations leading to efficient use of nitrogen. In this situation, an improvement of photosynthetic gain is expected even without any further investment of nitrogen. This idea was confirmed by theoretical studies (Woodrow, 1994; Medlyn, 1996). On the other hand, many experimental studies have suggested that the nitrogen reallocation among photosynthetic components is hardly affected by CO₂ levels in most C₃ species (Sage, 1994). However, it is also known that several species show a ‘beneficial’ response to elevated CO₂ levels (Sage, 1994). Very recently, Makino et al. (1997) investigated the nitrogen use efficiency of transgenic rice with decreased amounts of RuBPCase. They showed that the photosynthetic capacity of transgenic plants under high CO₂ concentration was higher than that of wild type when compared at the same nitrogen content. Thus, the optimal control of nitrogen partitioning can contribute to plant productivity in an environment with a high level of CO₂. This result also suggests that, in such a high CO₂ environment, the plants with reduced RuBPCase content, which are produced by biotechnology or mutation, can outperform plants adapted to the current CO₂ level.

Although several theoretical studies were conducted to predict optimal nitrogen partitioning among photosynthetic components under high CO₂ levels (Woodrow, 1994; Medlyn, 1996), the environmental conditions assumed in these studies were very restricted. In particular, temperature was assumed to be constant. Therefore, the effects of optimal nitrogen partitioning on CO₂ exchange at the global level are poorly understood. The aim of the present study is to estimate the quantitative contribution of optimization in the photosynthetic apparatus to plant productivity at the doubled CO₂ level under various environmental conditions. We use the model of Hikosaka (1997), which incorporates temperature dependence of the RuBP regeneration and the RuBPCase activity. We calculate leaf photosynthesis under various light, nutrition and temperature conditions at contrasting CO₂ levels.

Results of leaf photosynthesis are used to predict the optimal response of canopy photosynthesis to doubled CO₂. Distribution of nitrogen content among leaves in a canopy is known as a factor responsible for canopy photosynthesis: allocating the highest nitrogen content to the leaf exposed to the highest light leads to the maximum photosynthetic rate of the whole canopy (Field, 1983; Hirose and Werger, 1987). Optimal nitrogen distribution among leaves depends on the photosynthesis-nitrogen relationship (Anten et al., 1995). We further calculate optimal nitrogen distribution among leaves and photosynthesis of a canopy consisting of leaves whose photosynthetic apparatus is optimal or suboptimal at high CO₂ levels.
2. The model

In the present study, the model of Hikosaka (1997) is used. Equations are shown in the Appendix. Short-term responses of the photosynthetic rate to environmental factors are based on the model of Farquhar et al. (1980) with some modifications. The photosynthetic rate is given by a minimum of the RuBP-saturated and the RuBP-limited rate of photosynthesis. Photosynthetic components are classified according to their function. The RuBP-saturated rate is determined by the amount of RuBPCase (Group I), while the RuBP-limited rate under saturated light is limited by proteins in the RuBP regeneration process: electron carriers, coupling factor and Calvin cycle enzymes other than RuBPCase (Group II) and core complex of photosystem II (PSII core, Group III). The amount of cytochrome $f$ (Cyt $f$) is used for representation of the amount of Group II. The rate of RuBP regeneration at weak light (initial slope of the light-response curve of photosynthesis) is determined by leaf chlorophyll (chl) content (Gabrielsen, 1948). All the chl molecules are assumed to be bound either to PSII core, core complex and light harvesting complex of photosystem I (PSI, Group IV), or to the light harvesting complex of photosystem II (LHCII, Group V). The amount of PSI is assumed to be proportional to leaf chl content (Hikosaka and Terashima, 1995). The number of nitrogen molecules required for each group is calculated according to Hikosaka and Terashima (1995). Photosynthetic nitrogen is allocated among these groups. For example, to increase photosynthetic rates at low light, investment in chl-protein complexes (Group III–V) is advantageous (Hikosaka and Terashima, 1995). Investment in Group II and III is necessary to increase the capacity of RuBP regeneration at high light intensity.

Another limiting process, triose phosphate utilization (Sharkey, 1985), is ignored in the present study because it may not commonly limit photosynthetic rates if the sink-limitation is not considerable (Socias et al., 1993; Medlyn, 1996; Hikosaka, 1997).

The daily course of PFD is simply assumed to be a sine-square curve. Here, the maximum irradiance at noon, $I_0$, is regarded as an index of light availability. Leaf nitrogen content per unit leaf area, [N], may reflect nitrogen availability. Photosynthetic nitrogen content is a linear function of leaf nitrogen content. Daily temperature is assumed to be constant throughout the day, but Hikosaka (1997) already showed that fluctuation of temperature in a day has minor effects on optimal nitrogen partitioning. It is also assumed that there is no water deficit throughout a day.

3. Results

3.1. Effect of the optimal nitrogen partitioning on photosynthesis at the doubled CO$_2$ level

First, results under the condition at which daily temperature is 25°C throughout the day are presented. Fig. 1 shows dependence of the instantaneous rate of photosynthesis on the partial pressure of atmospheric CO$_2$ in leaves with opti-

![Fig. 1. CO$_2$ response curve of the instantaneous rate of photosynthesis of leaves at given $I_0$. Nitrogen partitioning is optimized at 35 Pa (dotted lines) and 70 Pa (solid lines) under respective $I_0$. Typical nitrogen contents for each $I_0$ are selected: [N] = 0.06, 0.12 and 0.18 mol m$^{-2}$ for $I_0$ = 200, 600 and 2000 $\mu$mol m$^{-2}$ s$^{-1}$. Circles indicate the photosynthetic rate at optimized CO$_2$ levels.](image)
Fig. 2. Daily photosynthesis versus leaf nitrogen content. (A) Dotted lines, photosynthesis at 35 Pa of a leaf optimal at 35 Pa; (B) broken lines, photosynthesis at 70 Pa of a leaf optimal at 35 Pa; (C) solid lines, photosynthesis at 70 Pa of a leaf optimal at 70 Pa. Numbers in the figure represent $I_0$s. 0 indicates daily respiration.

Fig. 3. (a) Ratio of daily photosynthesis versus leaf nitrogen content. Solid lines represent the ratio of photosynthesis at 70 Pa of a leaf optimal at 70 Pa to photosynthesis at 35 Pa of a leaf optimal at 35 Pa. Dotted lines represent the ratio of photosynthesis at 70 Pa and that at 35 Pa by a leaf optimal at 35 Pa. Symbols are as in (a).
piration) are calculated (Fig. 3(b)). In a leaf optimal at 35 Pa, gross photosynthesis at 70 Pa ($B'$) is 20–35% higher than that at 35 Pa ($A'$) at given [N] and $I_0$, and this tendency is similar among different $I_0$s. On the other hand, the ratio of gross photosynthesis at 70 Pa in a leaf optimal at 70 Pa ($C'$) to $A'$ is different depending on $I_0$s. At $I_0 = 2000$, $C'/A'$ is 1.4–1.5. However, at lower $I_0$s, $C'/A'$ decreases with increasing [N] and achieves a level similar to $B'/A'$.

Fig. 4 compares optimal amount of key components, Cyt f, RuBPCase and chl, at contrasting CO2 levels. The amount of Cyt f, which is a representative of the limiting factor of the RuBP regeneration rate, is greater at 70 Pa, while the amount of RuBPCase is less (Fig. 4(a) and (b)). The chlorophyll content, which determines the photosynthetic rate at low light, increases at 70 Pa (Fig. 4(c)). Relative partitioning of nitrogen among photosynthetic components is shown in Fig. 5. The proportion of RuBPCase decreases at 70 Pa while other components increase. Since the fractions of Group III, IV and V increase almost proportionately at 70 Pa, changes in chl $a/b$ ratio in the optimal partitioning, calculated according to Hikosaka and Terashima (1995), were very small (data not shown).

3.2. Interaction of CO2 and temperature

Fig. 6 shows daily photosynthesis at different temperatures under the two CO2 conditions. Nitrogen partitioning is optimized at each temperature under respective CO2 levels. Daily photosynthesis at 70 Pa in leaves optimized at 35 Pa is also shown. $I_0 = 2000$ and [N] = 0.18 are assumed. The peak of the curve shifts to higher temperature with increasing CO2 level. Although the nitrogen partitioning affects daily photosynthesis, it should be noted that the peak of the curve depends only on the CO2 level at measurement, not on the nitrogen partitioning. Fig. 7 shows that the ratio of daily photosynthesis at 70 Pa to that at 35 Pa increases with increasing temperature. The difference between $B/A$ and $C/A$ increases with increasing temperature.

![Fig. 4. Optimal content of photosynthetic components at two CO2 levels plotted against the leaf nitrogen content. (a) RuBPCase; (b) cyt f; (c) chl. Symbols are as in Fig. 1.](image)

3.3. Canopy photosynthesis

Here, we consider a very simple canopy that has three layers. Leaves at each layer receive 200, 600 or 2000 $\mu$mol m$^{-2}$ s$^{-1}$ at noon. Canopy photosynthesis is maximized when all leaves in the canopy satisfy the following equation:
\[ \frac{\partial P_{\text{day}}}{\partial [N]} = \lambda \]

where \( \lambda \) is a Lagrange multiplier (Field, 1983; Hirose and Werger, 1987). \( \frac{\partial P_{\text{day}}}{\partial [N]} \) is calculated for the photosynthesis-[N] relationship in leaves optimal at different CO\(_2\) levels based on the data shown in Fig. 2 (\( A, B \) and \( C \) as defined above). Fig. 8 shows optimal nitrogen allocation among leaf layers, which satisfies the above equation. Two nitrogen availabilities (mean [N]s of three leaf layers are 0.08 and 0.12 mol m\(^{-2}\)) are considered. In both nitrogen availabilities, the effect of CO\(_2\) and nitrogen partitioning among photosynthetic components on the optimal nitrogen distribution among leaf layers is negligibly small. Canopy photosynthesis increases by >60% with optimal reallocation of nitrogen among photosynthetic components and by 40% without changes in the nitrogen allocation (Table 2).

### 3.4. Sensitivity analysis

Effects on daily photosynthesis of changes in the values of the constants that may vary among species are examined (Fig. 9). The \( x \)-axis indicates relative values of each constant to the values assumed in the model (Table 1) and the \( y \)-axis represents changes in the photosynthesis when one constant changes with the other constants being unchanged (Fig. 9(a)). The assumed condi-

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Fig. 5. Optimal nitrogen partitioning among photosynthetic components at two CO\(_2\) levels (35 and 70 Pa) and at three irradiance levels (\( I_0 = 200, 600 \) and 2000). Nitrogen allocated to each group relative to photosynthetic nitrogen (\( N_p \)) is shown. Typical nitrogen contents for each \( I_0 \) are selected: [N] = 0.06, 0.12 and 0.18 mol m\(^{-2}\) for \( I_0 = 200, 600 \) and 2000 \( \mu \)mol m\(^{-2}\) s\(^{-1}\).

Fig. 6. Effects of CO\(_2\) level and temperature on optimized daily photosynthesis. Daily photosynthesis at 70 Pa of leaves optimized at 35 Pa and at the same temperature is also shown. \( I_0 = 2000 \ \mu \)mol m\(^{-2}\) s\(^{-1}\), [N] = 0.18 mol m\(^{-2}\).
4. Discussion

4.1. Photosynthetic acclimation to changes in CO₂ levels

Our model predicts that, at 25°C, daily photosynthesis of a leaf at 70 Pa under strong light is improved by 60% with optimal reallocation of nitrogen among photosynthetic components and by 40% without changes in the nitrogen allocation (Fig. 3). The effects of the optimal nitrogen partitioning for daily photosynthesis, however, change depending on irradiance and nitrogen content. At lower \( I_0 \), the optimization in the nitrogen partitioning is more effective at lower nitrogen contents, while the advantage in daily photosynthesis due to the optimal partitioning decreases with increasing \([N]\) (Fig. 3(b)). Daily photosynthesis has maxima at \([N]=0.1\) for \( I_0 = 200\) and \([N]=0.2\) for \( I_0 = 600\) (Fig. 2). Thus, when \([N]\) is lower than these values, daily photosynthesis is nitrogen limited, while it is light limited at higher \([N]\) (Hikosaka and Terashima, 1995; Terashima and Hikosaka, 1995; Hikosaka et al., 1998). When \([N]\) exceeds these optimal values, therefore, nitrogen is not a primary factor limiting photosynthesis and its optimal partitioning is less meaningful.

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Table 1

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<td>β</td>
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See Hikosaka (1997) for reference of each value. Also see Appendix I for abbreviations.

with increasing nitrogen content. However, she did not try to estimate the ratio at various PFDs.

The optimal nitrogen partitioning at 35 Pa differs from that at 70 Pa as indicated by previous studies (Hogan et al., 1991; Sage, 1994; Webber et al., 1994; Woodrow, 1994; Medlyn, 1996). The fraction of nitrogen in RubPCase decreases, while that of other fractions increases (Figs. 4 and 5). On the other hand, in optimal partitioning, the leaf chl content at 70 Pa is higher than that at 35 Pa (Fig. 4(c)), which was unexpected by the previous studies. This increase is interpreted as a compensation for the balance between the light-saturated rate and the initial slope of lightrresponse curve of photosynthesis. When allocation between Group I, II and III is optimized, the light-saturated rate of photosynthesis at 70 Pa is 60% higher than that at 35 Pa. Within this 60% increase, 40% is due to the increase of the CO$_2$ level and 20% is due to the change in nitrogen partitioning (Fig. 3). On the other hand, since the initial slope of light-response curve is limited by a single component, chl, the increase in the initial slope by doubling CO$_2$ is only 40% if the chl content is identical. Thus, to balance the light-saturated rate and the initial slope, partitioning of

![Diagram](image_url)
nitrogen to chl increases with increasing CO₂ level. On the other hand, if the reallocation of nitrogen between RuBP regeneration and the capacity of RuBPCase does not change with CO₂ levels, the increase in the light-saturated rate by doubling CO₂ is the same level in that in the initial slope. Therefore, changes in the chl content would not be necessary because the balance between the light-saturated rate and the initial slope does not change.

4.2. Applicability of the model

Not only nitrogen content but photosynthetic nitrogen use efficiency (PNUE, photosynthetic capacity per unit nitrogen) differs among species. Difference in PNUE among species has been attributed to the difference in the CO₂ level at the chloroplasts and in the fraction of nitrogen allocated to the photosynthetic apparatus (Lloyd et al., 1992; Hikosaka et al., 1998). The latter directly affects the absolute value of daily photosynthesis at a given nitrogen content but the presented prediction is qualitatively unaffected. The former difference would be due to the difference in CO₂ diffusion from the intercellular space to the chloroplasts (gₗ). In the presented model, gₗ is assumed to correlate with the content of RuBPCase (Evans et al., 1994). Sensitivity analysis suggests that the effect of changes in the regression coefficient of gₗ on the RuBPCase content (aₗ) is small (Fig. 9).

Sensitivity analysis showed that the kinetic properties of RuBPCase, i.e. Kᵣ, Kₒ and Vₒₘₐₓ/Vₑₘₐₓ, considerably affect daily photosynthesis and the increment of daily photosynthesis by CO₂ elevation (Table 2) (Fig. 9). When Γ* was assumed to be constant, however, even with varying Kᵣ, Kₒ and Vₒₘₐₓ/Vₑₘₐₓ, daily photosynthesis and C/A were less sensitive (data not shown). Therefore, the large effect of these parameters was due to the fact that they affected photosynthesis through change in Γ* (Appendix II). Since the difference in Γ* among C₃ species may be small (Brooks and Farquhar, 1985), the predicted values in our model may be applicable to many C₃ plants.

### Table 2
Effect of CO₂ elevation and photosynthetic acclimation on canopy photosynthesis per leaf area

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean [N] = 0.08 mol m⁻²</td>
<td>0.320</td>
<td>0.451</td>
<td>0.534</td>
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<tr>
<td>Canopy photosynthesis (Relative)</td>
<td>(1.00)</td>
<td>(1.41)</td>
<td>(1.67)</td>
</tr>
<tr>
<td>Mean [N] = 0.12 mol m⁻²</td>
<td>0.537</td>
<td>0.753</td>
<td>0.860</td>
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<tr>
<td>Canopy photosynthesis (Relative)</td>
<td>(1.00)</td>
<td>(1.40)</td>
<td>(1.60)</td>
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</table>

The hypothetical canopy consists of three leaf layers whose light conditions are expressed by square sine curves with I₀ = 200, 600 and 2000 μmol m⁻² s⁻¹. Three types of photosynthesis-nitrogen relationship are used: A. photosynthesis at 35 Pa by leaves optimal at 35 Pa; B. photosynthesis at 70 Pa by leaves optimal at 70 Pa; C. photosynthesis at 70 Pa by leaves optimal at 70 Pa (see also Fig. 2). The nitrogen content of each layer is adjusted to satisfy \( \bar{P}_{d_{\text{day}}}/[\text{N}] = 1 \) (Fig. 7). Unit of canopy photosynthesis is mol m⁻² d⁻¹. Two types of canopy with different nitrogen availabilities (mean [N]s of three layers are 0.08 and 0.12 mol m⁻²) are considered.

4.3. Interaction of CO₂ and temperature

The increase of daily photosynthesis by doubling the current CO₂ level is enhanced with increasing temperature (Figs. 6 and 7). This enhancement is due to suppression of photorespiration at higher CO₂ concentrations. Photorespiration is more sensitive to temperature than photosynthesis and is suppressed at high CO₂ levels. Due to these effects, the decrease of CO₂ exchange rates at higher temperatures is large at low CO₂ concentrations but becomes small with increased CO₂ concentrations. Consequently, the temperature optimum of daily photosynthesis shifts to higher temperatures with increasing CO₂ level (Fig. 6 (Long, 1991)).

Temperature dependence of the RuBP regeneration rate may differ among species (Hikosaka, 1997). However, when the contrasting temperature dependence of the RuBP regeneration rate was applied, it was found that it does not affect the ratio of daily photosynthesis at 70 Pa to that at 35 Pa (data not shown). This suggests that effects of CO₂ enrichment on the photosynthetic gain at given temperature may be similar among various C₃ species.
4.4. Canopy photosynthesis

If the leaf area index and nitrogen content in a canopy are fixed, canopy photosynthesis is determined by the photosynthesis-nitrogen relationship and by the nitrogen allocation among leaves (Hirose and Werger, 1987). As mentioned above, optimal nitrogen distribution among leaves depends on the photosynthesis-nitrogen relationship. However, although daily photosynthesis differs depending on CO2 levels and on optimization of the photosynthetic apparatus when compared at the same nitrogen content (Fig. 2), the effects of CO2 levels on the optimal nitrogen distribution within a canopy are predicted to be negligibly small (Fig. 8). This is due to that effect of CO2 levels and the optimization on the shape of the curve of the photosynthesis-nitrogen relationship is small. In fact, Hirose et al. (1997) showed that the nitrogen distribution among leaves was not influenced by CO2 levels in stands of Abutilon theophrasti and Ambrosia artemisiifolia. Thus, if the leaf area index and nitrogen content in a canopy are independent of the CO2 level, the increase in canopy photosynthesis may be very similar to that in leaf photosynthesis (Table 1). Although we found that the advantage to leaf photosynthesis due to the optimization of the photosynthetic apparatus decreases with increasing [N] at lower I0s (Fig. 3), the advantage to canopy photosynthesis is still high because nitrogen is less allocated to the leaves that receive lower PFDs (Fig. 8).

In stands of Abutilon theophrasti and Ambrosia artemisiifolia, leaf area index was not sensitive to CO2 levels but correlated to nitrogen content of the whole canopy (Hirose et al., 1996). They suggested that leaf area development of the stands was primarily determined by the amount of nitrogen taken from soil rather than CO2 levels. Ziska et al. (1996) also showed that leaf area development in rice stands greatly changed with nitrogen availability but was similar at different CO2 levels when nitrogen availability was similar. However, if elevation in the CO2 level decreases nitrogen availability in the ecosystem (Bazzaz, 1990), the leaf area index may decrease, which makes the prediction of primary production difficult.

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Appendix A

Abbreviations and units

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>a, b</td>
<td>Regression constants</td>
</tr>
<tr>
<td>CF</td>
<td>Coupling factor</td>
</tr>
<tr>
<td>chl</td>
<td>Chlorophyll</td>
</tr>
<tr>
<td>[Chl]</td>
<td>Leaf chl content (mmol m⁻²)</td>
</tr>
<tr>
<td>chlx</td>
<td>Number of chl molecules associated with chl-complex x (mol mol⁻¹)</td>
</tr>
<tr>
<td>cyt f</td>
<td>Cytochrome f</td>
</tr>
<tr>
<td>[Cyt f]</td>
<td>Leaf cyt f content (µmol m⁻²)</td>
</tr>
<tr>
<td>gw</td>
<td>Conductance of CO₂ from intercellular space to chloroplasts (mmol m⁻² s⁻¹ Pa⁻¹)</td>
</tr>
<tr>
<td>I</td>
<td>Incident photon flux density (µmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>I₀</td>
<td>I at noon (µmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>J</td>
<td>Rate of electron transport (µmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>Jmax</td>
<td>Light-saturated rate of electron transport (µmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>kcat</td>
<td>specific activity of RuBPCase (mol mol⁻¹ s⁻¹)</td>
</tr>
<tr>
<td>Ke, Ko</td>
<td>Michaelis constants for CO₂ and O₂, respectively (Pa, kPa)</td>
</tr>
<tr>
<td>LHC</td>
<td>Light harvesting chl-protein complex</td>
</tr>
<tr>
<td>[LHCII]</td>
<td>leaf LHCII content (µmol m⁻²)</td>
</tr>
<tr>
<td>[N]</td>
<td>Leaf nitrogen content (mol m⁻²)</td>
</tr>
<tr>
<td>Np</td>
<td>Nitrogen in photosynthetic components</td>
</tr>
<tr>
<td>[Np]</td>
<td>Leaf photosynthetic nitrogen content (mol m⁻²)</td>
</tr>
<tr>
<td>nx</td>
<td>Nitrogen molecule in group x (mol mol⁻¹)</td>
</tr>
</tbody>
</table>
\( O \) Partial pressure of O\(_2\) (kPa)

\( P \) Instantaneous rate of photosynthesis

\( p_a \) Partial pressure of ambient CO\(_2\) (Pa)

\( p_c \) CO\(_2\) level at chloroplast in terms of partial pressure (Pa)

\( P_{\text{day}} \) Daily rate of photosynthesis (mol m\(^{-2}\) d\(^{-1}\))

\( \text{PFD} \) Photon flux density

\( \text{PSI} \) Core complex of photosystem I and LHCI

\([\text{PSI}]\) Leaf PSI content (\(\mu\)mol m\(^{-2}\))

\( \text{PSII core} \) Core complex of photosystem II

\([\text{PSII}]\) Leaf PSII content (\(\mu\)mol m\(^{-2}\))

\( R \) Rate of dark respiration (mol m\(^{-2}\) s\(^{-1}\))

\( \text{RuBP} \) Ribulose-1,5-bisphosphate

\( \text{RuBPCase} \) Ribulose-1,5-bisphosphate carboxylase

\([\text{RuBPCase}]\) Leaf RuBPCase content (\(\mu\)mol m\(^{-2}\))

\( t \) Time of day (h)

\( V_{\text{cmax}} \) Maximum velocity of RuBP carboxylation (\(\mu\)mol m\(^{-2}\) s\(^{-1}\))

\( V_{\text{omax}} \) Maximum velocity of RuBP oxygenation (\(\mu\)mol m\(^{-2}\) s\(^{-1}\))

\( W_c \) RuBP-saturated rate of carboxylation (\(\mu\)mol m\(^{-2}\) s\(^{-1}\))

\( W_j \) RuBP-limited rate of carboxylation (\(\mu\)mol m\(^{-2}\) s\(^{-1}\))

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

\( \beta \) The ratio of \(p_t/p_a\)

\( \phi_t \) The initial slope of light response curve of the RuBP regeneration rate (mol mol\(^{-1}\))

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

**Photosynthetic rate**

The photosynthetic rate \( (P) \) is given by a minimum of the RuBP-saturated rate of photosynthesis \( (P_s) \) and the RuBP-limited rate of photosynthesis \( (P_l) \):

\[
P = \min\{P_s, P_l\}. \tag{A1}
\]

\( P_s \) and \( P_l \) are expressed as:

\[
P_s = \frac{V_{\text{cmax}}(p_c - \Gamma^*)}{p_c + K_c(1 + O/K_o)} - R \tag{A2}
\]

\[
P_l = \frac{J(p_c - \Gamma^*)}{4p_c + 8\Gamma^*} - R \tag{A3}
\]

where \( R \) is the dark respiration rate, \( V_{\text{cmax}} \) 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, \( K_c \) and \( K_o \) are the Michaelis constants for CO\(_2\) and O\(_2\), respectively, \( O \) is the partial pressure of O\(_2\). \( \Gamma^* \) is the CO\(_2\) compensation point in the absence of respiration defined as follows:

\[
\Gamma^* = \frac{0.5V_{\text{omax}}K_cO}{V_{\text{cmax}}K_o} \tag{A4}
\]

where \( V_{\text{omax}} \) is the maximum velocity of RuBP oxygenation per leaf area. \( J \) is the rate of electron transport on a leaf area basis, expressed as,

\[
J = \frac{\phi_t I + J_{\text{max}} - ((\phi_t I + J_{\text{max}})^2 - 4\phi_t I \theta J_{\text{max}})^{1/2}}{2\theta} \tag{A5}
\]

where \( I \) is the incident photon flux density (PFD), \( J_{\text{max}} \) is the light-saturated rate of \( J \), \( \phi_t \) is the initial slope of the curve, and \( \theta \) is the convexity of the curve. The partial pressure of intercellular CO\(_2\) \( (p_i) \) is assumed to be a constant fraction of that of atmospheric CO\(_2\) \( (p_a) \) independent of CO\(_2\) and temperature conditions (Sage, 1994)

\[
p_t = \beta p_a. \tag{A6}
\]

Then, \( p_c \) is given as,

\[
p_c = p_t - P/g_w \tag{A7}
\]

**Appendix B**

Here, equations used in the model are shown. See Appendix I for abbreviations and units. For detailed explanation of the model, see Hikosaka (1997).
where $g_w$ is the conductance for CO$_2$ from the intercellular space to the chloroplasts, which is assumed to be a function of the RuBPCase content,

$$g_{w25} = a_g[RuBPCase] + b_g$$  \hspace{1cm} (A8)

where the suffix $25$ means temperature at $25^\circ C$, $a$ and $b$ are constants (Table 1) and components in the 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 of photosynthetic components:

$$V_{cmax25} = k_{cat}[RuBPCase]$$  \hspace{1cm} (A9)

$$J_{max25} = a_f[cyt f] = a_p[PSII]$$  \hspace{1cm} (A10)

$$f_{ac}[chl] = \left( b_{c} [chl] \right)$$  \hspace{1cm} (A11)

where $k_{cat}$ is the specific activity of RuBPCase. The amount of PSI is assumed to be parallel to that of the chl content:

$$[PSI] = a_{[chl]}.$$  \hspace{1cm} (A12)

The amount of LHCII is estimated on the assumption that every chl molecule is bound either to the PSII core, to PSI, or to LHCII; thus,

$$[LHCII] = \left(1000[chl] - [chl]_{PSII}[PSII] - [chl]_{PSII}[PSII]\right)$$

$$/ [chl]_{LHCII}$$  \hspace{1cm} (A13)

where chl, denotes the number of chl molecules associated with chl-protein complex $x$ and 1000 is a factor for adjustments of the difference in the units.

Photosynthetic nitrogen, $N_p$, is a sum of nitrogen in all the components:

$$[N_p] = n_{[RuBPCase]} + n_{[cyt f]} + n_{[PSII]}$$

$$+ n_{[PSII]} + n_{[LHCII]}$$  \hspace{1cm} (A14)

where $n_x$ is the nitrogen cost (nitrogen molecule in each group) of group $x$. Since $[PSI]$ is a function of [chl] (Eq. (A12)), $[LHCII]$ is a function of $[PSII]$ and [chl]. By substituting Eq. (A10), Eq. (A12) and Eq. (A13) into Eq. (A14) with appropriate rearrangements, $[RuBPCase]$ is expressed as a function of $[N_p], [PSII]$ and [chl]. Therefore, the amount of each group is expressed as a function of $[N_p], [PSII]$ and [chl].

The leaf nitrogen content, $[N]$, is expressed as a function of $[N_p]$,

$$[N] = a_{[N_p]} + b_{[N]}.$$  \hspace{1cm} (A15)

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

$$R_{25} = a_{[N]} + b_{[N]}$$  \hspace{1cm} (A16)

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

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

$$I = 0 \quad (0 \leq t \leq 6, 18 \leq t \leq 24)$$  \hspace{1cm} (A17)

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

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

$$P_{day} = \int_0^{24} P dt.$$  \hspace{1cm} (A18)

**Temperature dependence**

Temperature dependence of the respiration rate is expressed as follows:

$$R = R_{25} \exp\left\{ E_a / R_{298.2} \right\} (1 - 298.2/T)$$  \hspace{1cm} (A19)

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

Temperature dependence of $g_w$ is assumed as follows:

$$g_w = g_{w25}(-6.81 + 0.0262 T).$$  \hspace{1cm} (A20)

The temperature dependences of $V_{cmax}, V_{omax}, K_c$, $K_o$, and $J_{max}$ are fitted by polynomial:

$$V_{cmax} = V_{cmax25}(-615.85 + 6.78 T - 0.0249474 T^2$$

$$+ 3.0677 \times 10^{-5} T^3).$$  \hspace{1cm} (21)

$$V_{omax} = V_{omax25}(-9.94 + 0.0367 T)$$  \hspace{1cm} (A22)

$$K_c = K_{c25}(-1654.72 + 17.748 T - 0.063526 T^2$$

$$+ 7.5884 \times 10^{-5} T^3)$$  \hspace{1cm} (A23)

$$K_o = K_{o25}(-4.05 + 0.0169 T)$$  \hspace{1cm} (A24)

$$J_{max} = J_{max25}\{1 + 0.0409(T - 298.2)$$

$$- 0.00154(T - 298.2)^2 - 9.42$$

$$\times 10^{-5}(T - 298.2)^3\}$$  \hspace{1cm} (A25)
As mentioned above, the amount of each component can be expressed as a function of three variables, \( [N] \), \([chl]\) and \([PSII]\). Therefore, combining all the equations, we can calculate \( P_{\text{day}} \) from \( T, I_o, p_a, [N], [chl] \) and \([PSII]\). The optimal combination of \([chl]\) and \([PSII]\) that maximizes \( P_{\text{day}} \) at given \([N] \), \( T \), \( p_a \) and \( I_o \) is calculated numerically.

References


