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A Model Describing the Regulation of Ribulose-1,5-Bisphosphate Carboxylase, Electron Transport, and Triose Phosphate Use in Response to Light Intensity and CO_2 in C_3 Plants[1]

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ABSTRACT

A model of the regulation of the activity of ribulose-1,5-bisphosphate carboxylase, electron transport, and the rate of orthophosphate regeneration by starch and sucrose synthesis in response to changes in light intensity and partial pressures of CO_2 and O_2 is presented. The key assumption behind the model is that nonlimiting processes of photosynthesis are regulated to balance the capacity of limiting processes. Thus, at CO_2 partial pressures below ambient, when a limitation on photosynthesis by the capacity of rubisco is postulated, the activities of electron transport and phosphate regeneration are down-regulated in order that the rate of RuBP regeneration matches the rate of RuBP consumption by rubisco. Similarly, at subsaturating light intensity or elevated CO_2, when electron transport or Pi regeneration may limit photosynthesis, the activity of rubisco is downregulated to balance the limitation in the rate of RuBP regeneration. Comparisons with published data demonstrate a general consistency between modelled predictions and measured results.

Biochemical explanations of the characteristics of photosynthesis in intact leaves often invoke limitations by one of three general processes: (a) the enzymatic capacity of rubisco (Table I), (b) the capacity of light harvesting, electron transport, and the photosynthetic carbon reduction cycle to regenerate RuBP; and (c) the capacity for starch and sucrose synthesis to metabolize the products of photosynthesis and regenerate Pi for photophosphorylation, and ultimately RuBP regeneration (4, 5, 25, 26). The rubisco capacity is generally limiting at light saturation and below normal $p(CO_2)$. The capacity of the thylakoid reactions (light harvesting, electron transport) to regenerate RuBP is limiting at either subsaturating light or high light and above normal $p(CO_2)$. The capacity of starch and sucrose synthesis generally limits photosynthesis at high light and high $p(CO_2)$. The conditions required to observe these limitations depend upon temperature, growth $p(CO_2)$, nutrient status, and species (11, 17, 19). In recent years, much work has focused on the regulatory relationship between rubisco activity, the rate of RuBP regeneration, and the rate of starch and sucrose synthesis following changes in light intensity, $p(CO_2)$, $p(O_2)$, or nitrogen nutrition (10, 13–16, 18, 23, 27, 28, 32, 33). In general, when one process becomes the predominant limitation on photosynthesis, the activity of nonlimiting processes appears to be regulated downward in order to maintain a balance between each step in the photosynthetic pathway. For example, reducing the light intensity or increasing $p(CO_2)$ leads to a limitation on photosynthesis by the capacity to regenerate RuBP. In response, rubisco is regulated downward to balance the limitation in the rate of RuBP regeneration (24). Sucrose synthesis also appears to be regulated downward following reductions in light intensity due in part to changes in the level of fructose 2,6-bisphosphate and in some cases by modulation of the activity of sucrose phosphate synthase (29–31). In contrast, decreasing $p(CO_2)$ can lead to a limitation in the rubisco capacity, causing the rate of electron transport to be regulated downward (28). These regulatory adjustments are accomplished within minutes of changes in light or $p(CO_2)$ and may enhance carbon gain by minimizing extremes of pH, thylakoid energization, or pool sizes of photosynthetic metabolites (16, 18, 25, 28). Farquhar and coworkers (4, 5) have developed a theoretical model to describe the behavior of photosynthesis limited by either rubisco capacity or the capacity of the thylakoid reactions to regenerate RuBP. In their model, the rate of electron transport reflects the capacity of the thylakoid reactions. Sharkey (25) modified this model to account for a limitation in the capacity to regenerate Pi. However, these models do not account for the regulation of rubisco, electron transport or starch and sucrose synthesis. If one assumes that the photosynthetic apparatus is regulated so that the activity of nonlimiting components balance the capacity of limiting components, then the Farquhar *et al.* and Sharkey models can be adapted to model the light and $p(CO_2)$ response of the regulation of rubisco, electron transport, and the rate of triose phosphate use by starch and sucrose synthesis. In the present paper, a model is presented that describes the regulation of rubisco, electron transport, and triose phosphate use in response to changes in light intensity and $p(CO_2)$. In a companion paper (20), results are presented which test some of the predictions of the model.

Model Development

The key premise of the model is the photosynthetic biochemistry in the steady state is regulated so the rate at which

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Table I. *Abbreviations Used in This Paper*

rubisco,	ribulose-1,5-bisphosphate carboxylase (EC 4.1.1.39)
A,	net CO_2 assimilation rate
C,	CO_2 concentration in the stroma
C_i,	intercellular partial pressure of CO_2
J,	electron transport rate
J'_{max},	regulated maximum rate of electron transport
J_{max},	maximum electron transport rate
K_c,	Michealis constant of rubisco for CO_2
k_{cat},	catalytic turnover rate of an enzyme
K_o,	Michealis constant of rubisco for O_2
O,	O_2 concentration in the stroma
$p(CO_2)$,	partial pressure of CO_2
PFD,	photon flux density
$p(O_2)$,	partial pressure of O_2
R,	RuBP use rate
R_c,	RuBP use rate when CO_2 assimilation is limited by rubisco capacity
R_j,	RuBP use rate when CO_2 assimilation is limited by electron transport
R_t,	RuBP use rate when CO_2 assimilation is limited by triose phosphate use
R_d,	the rate of non-photorespiratory respiration
RuBP,	ribulose 1,5-bisphosphate
T,	triose phosphate use rate
T',	regulated rate of triose phosphate use
TPU,	triose-phosphate-use
V_{cmax},	maximum substrate saturated rate of rubisco carboxylation
V'_{cmax},	substrate saturated rate of downregulated rubisco
W_c,	rubisco-limited rate of carboxylation
W_j,	electron-transport-limited rate of carboxylation
W_t,	P_i-regeneration-limited rate of carboxylation
W',	indicates regulated rate of carboxylation
Γ_*,	the CO_2 compensation point in the absence of non-photorespiratory respiration

rubisco consumes RuBP equals the rate at which RuBP is regenerated. According to Farquhar and von Caemmerer (4) the rate of RuBP use (R) equals

$$R = V_c + V_o \tag{1}$$

where V_c is the carboxylation rate and V_o is the rate of oxygenation. When limited by rubisco, R can be described as

$$R_c = W_c + V_o \tag{2}$$

where W_c is the rubisco limited rate of carboxylation. When A is limited by the thylakoid reactions or the Pi-regeneration capacity, the rate of RuBP use equals the maximum rate of RuBP regeneration possible for a given set of conditions. When the thylakoid reactions are limiting, the rate of RuBP regeneration reflects the electron transport rate (4) and the RuBP use rate equals

$$R_j = W_j + V_o \tag{3}$$

where W_j is the electron-transport-limited rate of carboxylation. When Pi-regeneration is limiting, the rate at which rubisco consumes RuBP equals

$$R_t = W_t + V_o \tag{4}$$

where W_t is the Pi-regeneration-limited rate of carboxylation. The term $R_c = R_j = R_t$ is equivalent to $W_c = W_j = W_t$ because V_o cancels out.

If photosynthesis is regulated so that the rates of RuBP consumption, electron transport and Pi regeneration are balanced then one of the following holds:

(a) If $W_j < W_c$ and $W_j < W_t$, then $W'_c = W'_t = W_j$ where W'_c equals the downregulated capacity of rubisco ($W'_c < W_c$), and W'_t equals the regulated rate of Pi regeneration.

(b) If $W_c < W_j$ and $W_c < W_t$ then $W'_j = W'_t = W_c$, where W'_j is the regulated rate of electron transport.

(c) If $W_t < W_c$ and $W_t < W_j$ then $W'_c = W'_j = W_t$.

From Farquhar and von Caemmerer (4) the rubisco limited rate of carboxylation equals

$$W_c = \frac{V_{cmax}(C)}{C + K_c(1 + O/K_o)} \tag{5}$$

where V_{cmax} is the potential maximum velocity of fully activated rubisco that is inhibitor free, C is the CO_2 concentration in the stroma, O is the O_2 concentration in the stroma, K_c is the Michaelis constant of rubisco for CO_2, and K_o is the Michaelis constant for O_2. The regulated rate of rubisco carboxylation equals

$$W'_c = \frac{V'_{cmax}(C)}{C + K_c\,(1 + O/K_o)} \tag{6}$$

where V'_{cmax} is the maximum velocity of downregulated rubisco.

If J is the potential rate of electron transport under a given set of conditions, Farquhar and von Caemmerer (4) define W_j as

$$W_j = \frac{J}{4.5 + 10.5\,(\Gamma_*/C)} \tag{7}$$

when ATP production limits RuBP regeneration. It is assumed that no ATP is required for the synthesis of starch or sucrose from triose phosphates. The term Γ_* is the CO_2 compensation point in the absence of non-photorespiratory respiration. The regulated rate of electron-transport-limited carboxylation then equals

$$W'_j = \frac{J'}{4.5 + 10.5\,(\Gamma_*/C)} \tag{8}$$

where J' is the regulated electron transport rate.

According to Sharkey (25), the rate of A limited by Pi regeneration equals

$$A = 3T - R_d \tag{9}$$

where T is the rate of triose phosphate use and R_d is the rate of nonphotorespiratory respiration. Photosynthesis limited by the rate of Pi regeneration equals (modifying Eq. 16.57 in Farquhar and von Caemmerer [4] for W_t)

$$A = W_t(1 - \Gamma_*/C) - R_d \tag{10}$$

Substituting and solving

$$W_t = \frac{3T}{(1 - \Gamma_*/C)} \tag{11}$$

The regulated rate of Pi regeneration, W'_t equals

$$W'_t = \frac{3T'}{(1 - \Gamma_*/C)} \quad (12)$$

where T' is the regulated rate of triose phosphate use.

When W_j is limiting,

$$W'_c = \frac{V'_{cmax}(C)}{C + K_c(1 + O/K_o)} = W_j \quad (13)$$

rearranging

$$V'_{cmax} = \{C + K_c(1 + O/K_o)\}W_j/C \quad (14)$$

Similarly,

$$W'_t = 3T'/(1 - \Gamma_*/C) = W_j \quad (15)$$

giving

$$T' = (1 - \Gamma_*)W_j/3 \quad (16)$$

Using the same logic, when W_c is limiting,

$$J' = W_c(4.5 + 10.5\Gamma_*/C) \quad (17)$$

and

$$T' = (1 - \Gamma_*/C)W_c/3 \quad (18)$$

When W_t is limiting

$$V'_{cmax} = \{C + K_c(1 + O/K_o)\}W_t/C \quad (19)$$

and

$$J' = W_t(4.5 + 10.5\Gamma_*/C) \quad (20)$$

In the absence of effectors such as 2-carboxyarabinitol 1-phosphate, the ratio V'_{cmax}/V_{cmax} would reflect the activation state of the enzyme, which is primarily dependent on the degree of carbamylation of rubisco (3). When effectors are present, V'_{cmax}/V_{cmax} reflects the ratio of the initial k_{cat} (catalytic turnover rate of rubisco active sites in rapidly extracted and assayed leaf material) to the total k_{cat} (maximum catalytic turnover rate of fully activated, inhibitor free enzyme; 10). The ratio of initial to total k_{cat} reflects the regulatory state of the enzyme, termed here the activity ratio. Similarly, the ratios J'/J and T'/T reflect the regulatory state, or activity ratio, of electron transport and Pi regeneration, respectively.

In an optimal system, the limiting component of photosynthesis would operate at the maximum, fully activated rate possible given the external conditions. In this case, $V'_{cmax} = V_{cmax}$ if rubisco capacity is limiting, $J' = J$ if electron transport is limiting, and $T' = T$ if the capacity of triose phosphate use is limiting.

Using the equations above and from Farquhar and von Caemmerer (4) the rate of rubisco-limited A, electron-transport-limited A, Pi-regeneration-limited A, and the regulation of each of these processes was modeled in response to photon flux density, $p(CO_2)$, and $p(O_2)$. The triose phosphate use rate was assumed to be independent of direct effects of light, $p(CO_2)$, and $p(O_2)$. This is probably an oversimplification (31). Because there is as yet no theoretical way to model the relationship between T and light, $p(CO_2)$, or $p(O_2)$, the simplifying assumption was used. In the calculations, the following were assumed: leaf temperature is 25°C, and 80% of the incident light is absorbed and utilized by the light reactions. The relationship between J_{max} (the potential maximum rate of light saturated electron transport) and J was calculated according to Farquhar and Wong (6). The value of Γ_* was derived from Brooks and Farquhar (2). K_c values are from spinach (8). K_o was assumed to equal 400 μbar, a value reported for spinach (1). Henry's constants for CO_2 and O_2 (7) were used to convert between partial pressure and aqueous molar concentrations. All calculations were conducted using stromal solution concentrations. Stromal CO_2 concentrations were then converted to intercellular partial pressure assuming a mesophyll transfer conductance of 1 mol m^{-2} s^{-1}.

RESULTS

Light Response of Photosynthesis

In Figure 1, the modeled light responses of (a) the rate of CO_2 assimilation, (b) the ratio of the capacity of RuBP regeneration to the capacity of RuBP consumption, and (c) the activity ratios of rubisco, electron transport, and Pi regeneration are presented. Responses were modeled at a C_i of 230 μbar (Fig. 1, A, B, and C) or 100 μbar (Fig. 1, D, E, and F). The V_{cmax} of rubisco was assumed to be 130 μmol m^{-2} s^{-1}; J_{max} was assumed to be 350 μmol m^{-2} s^{-1}, and the triose phosphate use rate was set at 15 μmol m^{-2} s^{-1} which was

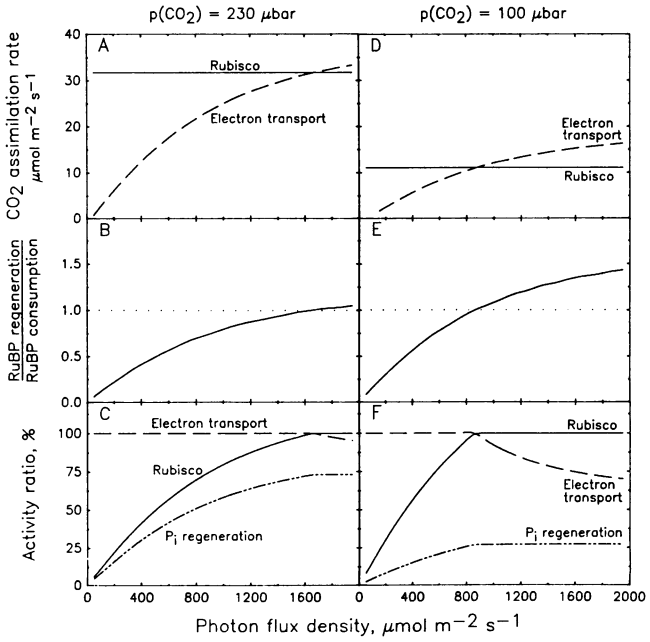

Figure 1. Modeled light responses at a $p(O_2)$ of 200 mbar of (a) the rate of net CO_2 assimilation limited by rubisco capacity or the capacity of electron transport (panels A and D), (b) the ratio of the capacity of RuBP regeneration relative to the capacity of RuBP consumption (panels B and E), and (c) the activity ratios of rubisco, electron transport, or Pi regeneration (panels C and F). Activity ratios reflect the actual, regulated rate of a process relative to the potential maximum rate possible under the given conditions. Responses modeled at a stromal $p(CO_2)$ of either 230 μbar (panels A, B, C) or 100 μbar (panels D, E, F). In panels B and E, dotted lines delineate where the RuBP consumption and RuBP regeneration capacities are equal. See text for model inputs.

nonlimiting in this example. In Figure 1, A and D for example, A at any given C_i would equal the minimum of the rubisco, electron transport, or Pi-regeneration-limited rate of photosynthesis at that C_i.

At a stromal CO_2 concentration equivalent to a C_i of 230 μbar, the assimilation rate increases with increasing PFD up to 1620 μmol m^{-2} s^{-1} (Fig. 1A), reflecting the limitation on A due to the capacity for electron transport. At 1620 μmol m^{-2} s^{-1}, rubisco becomes limiting, and the light saturation point is reached. Actual light saturation points are rarely as sharp as in Figure 1A principally because most leaves have a heterogeneous population of chloroplasts (12).

The ratio of the capacities of RuBP regeneration to RuBP consumption reflects the ratio of W_c to either W_j or W_t, whichever is smaller. When this ratio is less than one, rubisco capacity is in excess and rubisco is down-regulated to maintain a balance between the actual rate of RuBP regeneration and consumption occurring *in vivo* during steady-state photosynthesis (*cf.* Fig. 1, B and C). When the ratio is above one, rubisco is limiting and the rates of electron transport and starch and sucrose synthesis are down-regulated. In Figure 1B, the ratio of the capacity of RuBP regeneration to the capacity of RuBP consumption increases with increased light availability, reflecting the increased rate of electron transport. When rubisco becomes limiting, this ratio increases above one as increased PFD increases the potential rate of electron transport. In response, the activity ratio of electron transport is predicted to decrease as the PFD increases above the light saturation point. Lowering the C_i to 100 μbar reduces the capacity of rubisco to consume RuBP because of a deficiency of CO_2. As a result, rubisco is predicted to become limiting at lower PFD, the light saturation point correspondingly falls to near 800 μmol m^{-2} s^{-1} (*cf.* Fig. 1, A and D), and the ratio of the RuBP regeneration to RuBP consumption capacity is increased at any given PFD (Fig. 1, B and E). The PFD at which the rate of electron transport begins to down-regulate is reduced by the decrease in C_i (Fig. 1, C and F), and at any given PFD above the light saturation point, J is predicted to be lower at low C_i than high C_i. Data from Sharkey *et al.* (28) support this prediction.

The activity ratio of Pi regeneration is also strongly light dependent, reflecting the rate at which triose phosphates become available (Fig. 1, C and F). Reducing C_i lowers the activity ratio of Pi regeneration because the rate of triose phosphate production by rubisco is reduced, and the capacity of starch and sucrose synthesizing enzymes are downregulated to balance the rate of triose phosphate consumption with production.

CO_2 Response of Photosynthesis at 200 μbar O_2

In Figure 2, the modeled CO_2 responses of (a) CO_2 assimilation, (b) the ratio of the RuBP regeneration and consumption capacities, and (c) the activity ratio of rubisco, electron transport, and triose phosphate use are modeled using the same parameters as in Figure 1. The PFD was set at 1800 μmol m^{-2} s^{-1} (Fig. 2, A, B, and C) or 700 μmol m^{-2} s^{-1} (Fig. 2, D, E, and F). In this simulation, at 1800 μmol photons m^{-2} s^{-1} rubisco limits A at a C_i below 280 μbar, electron transport limits A between 280 and 540 μbar, and Pi regeneration limits

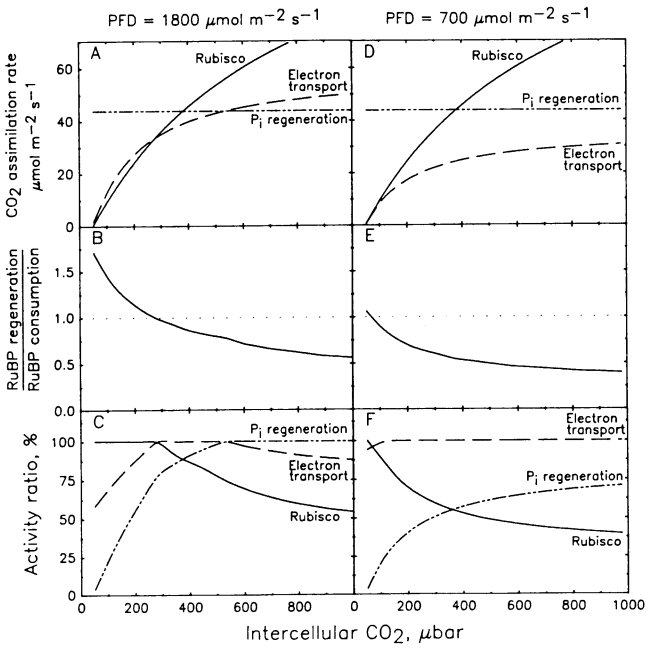

Figure 2. Modeled CO_2 responses at a $p(O_2)$ of 200 mbar of (a) the rate of CO_2 assimilation of rubisco, electron transport, or Pi-regeneration-limited photosynthesis (panels A and D), (b) the ratio of the capacity of RuBP regeneration to the capacity for RuBP consumption (panels B and E), and (c) the activity ratios of rubisco, electron transport, or Pi regeneration (panels D and F). Responses modeled at a photon flux density (PFD) of either 1800 μmol m^{-2} s^{-1} (panels A, B, C) or 700 μmol m^{-2} s^{-1} (panels D, E, F). Dotted lines in panels B and E as in Figure 1.

A above 540 μbar (Fig. 2, A, B, C). As the C_i falls below 280 μbar, the RuBP regeneration to consumption ratio increases above one because rubisco is increasingly limited by CO_2 (Fig. 2B). As the C_i increases above 280 μbar, the ratio of RuBP regeneration to consumption falls below one, because the increase in CO_2 gives rubisco the potential to consume RuBP faster than it can be regenerated. To maintain a balance, the model predicts the rate of electron transport will be down-regulated below a C_i of 280 μbar, and rubisco to be down-regulated above 280 μbar (Fig. 2C). The Pi regeneration rate is down-regulated below a C_i of 540 μbar and is fully activated above this C_i where it is predicted to be limiting. When Pi regeneration is limiting, the activity ratio of rubisco is predicted to decline faster with increasing C_i than occurs when electron transport is limiting, causing a slight inflection in the CO_2-response of the activity ratio of rubisco (Fig. 2C). This is because RuBP availability increases slightly with increasing C_i when electron transport limits, but not when Pi regeneration is limiting (25).

At reduced PFD (700 μmol m^{-2} s^{-1}), the rate of electron transport becomes limiting at nearly all C_i (Fig. 2D), and the RuBP regeneration-to-consumption ratio is reduced at all C_i (Fig. 2E). The activity ratio of both rubisco and Pi regeneration is lower at any given C_i than predicted at high PFD (Fig. 2, C and F). Unlike at a PFD of 1800 μmol m^{-2} s^{-1}, Pi regeneration never becomes limiting and the response of the activity ratio of Pi regeneration reflects the increase in

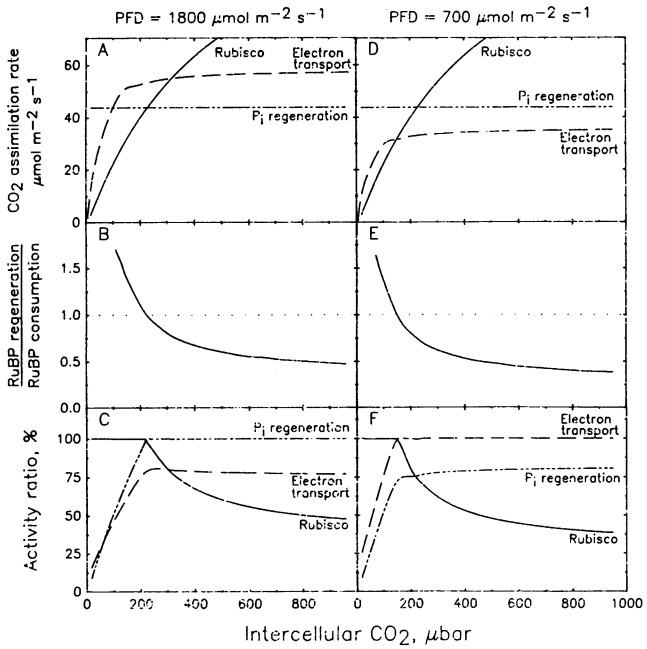

Figure 3. Modeled CO_2 responses at a $p(O_2)$ of 20 mbar of (a) the rate of CO_2 assimilation of rubisco, electron transport, or Pi-regeneration-limited photosynthesis (panels A and D), (b) the ratio of the capacity of RuBP regeneration to the capacity of RuBP consumption (panels B and E), and (c) the activity ratios of rubisco, electron transport, or Pi regeneration (panels D and F). Responses modelled at a photon flux density of either 1800 μmol m^{-2} s^{-1} (panels A, B, C) or 700 μmol m^{-2} s^{-1} (panels D, E, F). Dotted lines in panels B and E as in Figure 1.

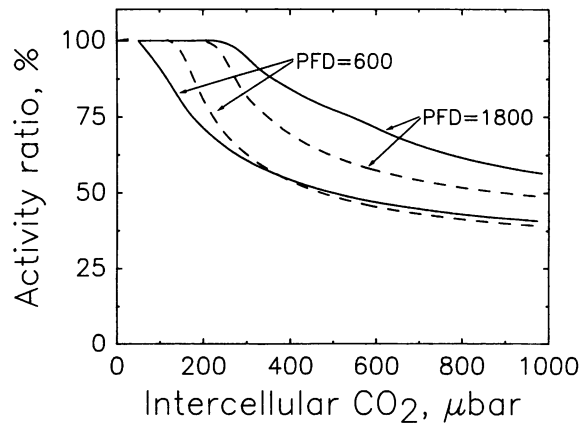

Figure 4. Modeled CO_2 responses of the activity ratio of rubisco at a photon flux density (PFD) of either 1800 μmol m^{-2} s^{-1} or 600 μmol m^{-2} s^{-1} and a $p(O_2)$ of either 200 mbar (solid lines) or 20 mbar (dashed lines). Modeled input as described in text except as follows: rubisco V_{cmax} = 100 μmol m^{-2} s^{-1}, J_{max} = 240 μmol m^{-2} s^{-1}, triose-phosphate use rate = 12 μmol m^{-2} s^{-1}. These inputs were used to model conditions found in *P. vulgaris* in order to compare modelled outputs against results published by Sharkey *et al.* (27; see text for comparison).

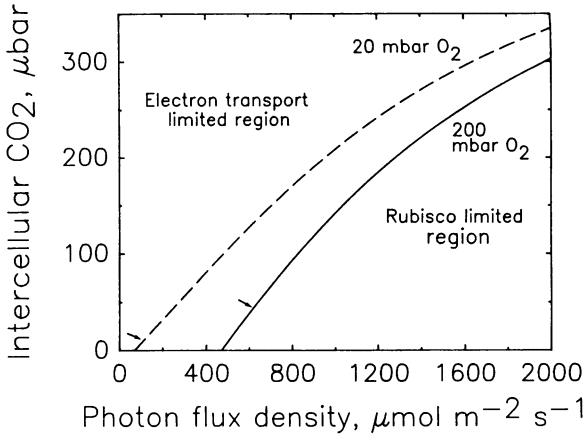

Figure 5. Effect of photon flux density on the intercellular $p(CO_2)$ at which the potential rubisco capacity equals the potential electron transport capacity at a $p(O_2)$ of 200 mbar (solid line) or 20 mbar (dashed line). Conditions are identical to those in Figures 2A and 3A except the Pi regeneration capacity was nonlimiting. Arrows indicate CO_2 compensation points.

h the electron-transport-limited rate of A with increasing C_i (Fig. 2F).

CO_2 Response of Photosynthesis at 20 mbar O_2

In Figure 3, the modeled CO_2 responses of (a) CO_2 assimilation, (b) the ratio of the RuBP regeneration to RuBP consumption capacities, and (c) the activity ratio of rubisco, electron transport, and Pi regeneration at 20 mbar $p(O_2)$ are presented. Conditions are identical to Figure 2 except for low $p(O_2)$. In comparison to results at 200 mbar $p(O_2)$, at 20 mbar and a PFD of 1800 μmol m^{-2} s^{-1}, the C_i where RuBP regeneration equals RuBP consumption and above which rubisco becomes nonlimiting has fallen to 220 μbar (Fig. 3, A and B). This occurs because reducing $p(O_2)$ stimulates both the rubisco and electron-transport-limited rates of A but not the Pi-regeneration-limited rate, thus Pi regeneration limits A at 220 μbar and above. As a result, at 20 mbar $p(O_2)$, the activity ratios of rubisco and electron transport begin to decline at a lower C_i than is the case at 200 mbar (*cf.* Figs. 2C and 3C). At any C_i above 220 μbar, the activity ratios of rubisco and electron transport are lower at 20 mbar than 200 mbar $p(O_2)$. This is also demonstrated in Figure 4 for a different set of modeled conditions (*cf.* solid and dashed lines representing responses at a PFD of 1800 μmol m^{-2} s^{-1}). If a Pi regeneration limitation is not evident, as is the case at a reduced PFD, than reducing $p(O_2)$ does not lead to a reduction in the activity ratio of rubisco, and may even stimulate it below a C_i of 300 μbar (Fig. 3, D, E, and F; Fig. 4).

Light Response of the Transition between Rubisco and Electron Transport Limited Regions

In Figure 5, the C_i at which the potential rubisco capacity balances the potential capacity for electron transport is modeled as a function of light intensity. For the conditions used in Figures 2A and 3A (with the exception that the Pi regen-

eration capacity was nonlimiting), Figure 5 demonstrates that as PFD falls, this balancing C_i declines. Below a C_i of 350 μbar, lowering $p(O_2)$ in the absence of a Pi regeneration limitation shifts the relationship to lower PFD. Thus, at constant PFD and C_i, when electron transport is limiting, reducing $p(O_2)$ should lead to a greater activity ratio of rubisco. If rubisco is limiting, reducing $p(O_2)$ should further reduce the activity ratio of electron transport.

DISCUSSION

The model presented here describes how rubisco, electron transport, and starch and sucrose synthesis would be regulated if the capacities of nonlimiting components within the photosynthetic apparatus were modulated to match the primary limitation on the rate of photosynthesis. Much evidence supports the predictions of the model. For example, it has been well established that reducing PFD below the light saturation point or increasing C_i above ambient leads to a reduction in the activity ratio of rubisco (10, 15, 16, 18, 27, 32, 33; see also reviews 21, 24, 34). Decreasing PFD is predicted to reduce the C_i at which rubisco is fully activated, while reducing C_i reduces the PFD at which rubisco is fully active (Figs. 1, 2, 4). In a companion paper, Sage *et al.* (20) confirm these predictions.

The model predicts that at light saturation, reducing C_i below ambient leads to a rubisco limitation and a decline in the rate of electron transport. Using pulse-modulated fluorescence to estimate the rate of electron transport *in vivo,* Sharkey *et al.* (28) demonstrate that J does decline as C_i is reduced below ambient in *Phaseolus vulgaris.* Also they show that when a Pi regeneration limitation is evident [high $p(CO_2)$ and light saturation], the rate of electron transport declines as C_i is increased in bean. This is not observed at subsaturating light, when electron transport, not Pi regeneration, limits photosynthesis.

According to the model, reducing $p(O_2)$ from 200 to 20 mbar should down-regulate rubisco when a Pi regeneration limitation is present, but when a Pi regeneration limitation is not evident, reducing $p(O_2)$ should enhance the activity ratio of rubisco at low C_i (if it is less than 100%) and have little effect at elevated C_i (Fig. 4). In agreement, Sharkey *et al.* (27), using bean (*P. vulgaris*), observed a decline in the activation state of rubisco at high C_i and saturating light (when a Pi regeneration limitation is postulated) but not at subsaturating PFD. Similarly, following a reduction in $p(O_2)$, Schnyder *et al.* (23) found rubisco to deactivate at 5°C, but not at 24°C. Low temperatures promote a Pi regeneration limitation (11, 17). Furthermore, in the presence of a Pi regeneration limitation, reducing the partial pressure of O_2 is predicted to down-regulate the rate of electron transport (*cf.* Figs. 2C and 3C). This was found to be the case in bean (28).

Single Limitation or Colimitation

The above model assumes that one of three general processes of the photosynthetic biochemistry is limiting A at any given environmental condition. This assumption is disputed (see contrasting arguments by Sharkey [26] and Woodrow and Berry [34]). Biochemical systems are widely noted as having the rate limitation spread out over numerous steps. That is, each step has some degree of control over the reaction (9). This view is not necessarily contrary to that assumed in this model. First, of the three processes thought to limit photosynthesis, only one, the rubisco limitation, is a single step process. This model does not assume that any single step within the processes of electron transport or Pi regeneration is limiting, only that the process itself is. Second, plants are largely at the mercy of the external environment, and sudden changes in the environment could push the system to the point where a single process is the principal limitation. In other words, the control on the reaction may disproportionately reside in one process. Time-course studies of the response of photosynthesis to changes in light intensity or $p(CO_2)$ support this interpretation (14, 19). The regulatory response of photosynthesis described in this model acts to realign the activities of nonlimiting with limiting processes, and by doing so reestablish the condition where the control is distributed throughout the photosynthetic pathway. However, while the activity of each component in the system may be balanced in the steady state, and therefore equally limiting photosynthesis in an immediate sense, the ultimate limitation will reside with the enzymes which are working at full capacity and have not been deactivated through regulatory fine tuning. In an ecological sense, the condition where one component of photosynthesis is always down-regulated would represent a waste of resources and would warrant a reallocation of resources from nonlimited and down-regulated processes to limiting processes. This model could be useful in predicting the optimal allocation shift following an environmental change.

CONCLUSION

Many studies have focused on the effect of the environment on the activation state of rubisco (for example 13, 16, 19, 23, 35). Great significance is often placed on findings which report differences in the activation state, although the meaning of these differences are frequently unknown. If it is correct that rubisco is regulated to balance a limitation elsewhere in the photosynthetic apparatus, then changes in the activation state may reflect a secondary response to the environment and not a direct response of rubisco itself. Similarly, changes in the regulatory state of electron transport or starch and sucrose synthesis may result from indirect effects. By modeling the regulation of rubisco, electron transport and P-regeneration, it is possible to see when changes in the activity ratio of these components reflect regulatory responses to limitations elsewhere in the photosynthetic apparatus. When changes in the activity ratio deviate substantially from the modeled predictions, it is possible that the regulatory control of the photosynthetic apparatus has lost effectiveness, and the change in the activity ratio may lead to a direct limitation of photosynthesis by that component.

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