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Limiting Factors in Photosynthesis

V. PHOTOCHEMICAL ENERGY SUPPLY COLIMITS PHOTOSYNTHESIS AT LOW VALUES OF INTERCELLULAR CO_2 CONCENTRATION

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ABSTRACT

Although there is now some agreement with the view that the supply of photochemical energy may influence photosynthetic rate (*P*) at high CO_2 pressures, it is less clear whether this limitation extends to *P* at low CO_2. This was investigated by measuring *P* per area as a function of the intercellular CO_2 concentration (C_i) at different levels of photochemical energy supply. Changes in the latter were obtained experimentally by varying the level of irradiance to normal (Fe-sufficient) leaves of *Beta vulgaris* L. cv F58-554H1, and by varying photosynthetic electron transport capacity using leaves from Fe-deficient and Fe-sufficient plants. *P* and C_i were determined for attached sugar beet leaves using open flow gas exchange. The results suggest that *P*/area was colimited by the supply of photochemical energy at very low as well as high values of C_i. Using the procedure developed by Perchorowicz *et al.* (Plant Physiol 1982 69:1165–1168), we investigated the effect of irradiance on ribulose bisphosphate carboxylase (RuBPCase) activation. The ratio of initial extractable activity to total inducible RuBPCase activity increased from 0.25 to 0.90 as leaf irradiance increased from 100 to 1500 microeinsteins photosynthetically active radiation per square meter per second. These data suggest that colimitation by photochemical energy supply at low C_i may be mediated via effects on RuBPCase activation.

Several researchers have used the relationship between CO_2 assimilation and CO_2 concentration to elucidate the factors controlling photosynthetic rate. Laing *et al.* (20) observed that P[1] was linearly related to the ambient CO_2 concentration from Γ to CO_2 saturation and concluded that *P* was limited by the concentrations of CO_2 and O_2, and by the kinetic parameters of RuBPCase. Other researchers have studied the relationship between P and intercellular CO_2 concentration (C_i) (9, 10, 12, 17, 18, 30). Farquhar *et al.* (13) obtained P/C_i curves under specific environmental conditions and interpreted these data in terms of the characteristics of biochemical systems. They concluded that there are two domains of photosynthetic limitation: the first relates to the initial slope of the P/C_i curve where *P* is dominated by the kinetic parameters of RuBPCase and the concentrations of CO_2 and O_2; the second relates to the plateau region of the P/C_i curve where *P* increases relatively less with increase in C_i and represents a condition which is proposed to be controlled by the supply of photochemical energy (*e.g.* ATP, NADPH).

An alternative view to the two-domain theory, one domain operating at low CO_2 and the other at high CO_2, is that photochemical energy supply may colimit P over the entire range of C_i values. The most recent report in this series (28) indicated that photochemical energy supply may colimit photosynthesis at ambient CO_2 concentrations of 300 μl l^{-1} or more; however, it was not clear whether this colimitation extended to very low CO_2 concentrations as well (28). In the present work, we explored this question further by (a) measuring P/C_i curves for leaves exposed to different levels of irradiance, and (b) determining P/C_i curves for leaves with different photosynthetic electron transport capacities using Fe-sufficient and Fe-deficient plants. Since we found that decreasing the supply of photochemical energy by either procedure led to a reduction in the initial slope of the P/C_i curve, we also explored the possibility that the effect of photochemical energy supply may be mediated via the level of activation of RuBPCase as suggested by Perchorowicz *et al.* (23).

MATERIALS AND METHODS

Plant Culture. Sugar beet plants (*Beta vulgaris* L. cv F58-554H1) were grown hydroponically in growth chambers and Fe deficiency was induced by transferring plants to culture solution without Fe as described previously (27).

Leaf Gas Exchange. *P*/area, leaf conductance, and C_i of individual attached leaves were determined over a range of ambient CO_2 concentrations using open flow gas exchange as described previously (see 28). The measurements were made by exposing the leaf initially to an ambient CO_2 concentration of about 1000 μl l^{-1} for 1.5 h at 21% O_2, then for 30 min at 1% O_2; subsequently, the ambient CO_2 concentration was lowered to successive levels with 30-min periods at 21% and 1% O_2 at each ambient CO_2 level. Leaf temperature was maintained at 30 ± 0.5°C. Irradiance was held either at a constant level (Fig. 2) or increased gradually to achieve light saturation at each CO_2 level (Fig. 4).

Photosynthetic Electron Transport. Chloroplasts were isolated from chilled leaves by a brief (5 s) homogenization in a Waring Blendor with an extraction solution of 50 mM Tricine (pH 7.8), 400 mM sorbitol, 10 mM NaCl, 5 mM $MgCl_2$, 1% (w/v) PVP-40, 0.2% (w/v) Na ascorbate, and 0.1% (w/v) BSA, at 4°C. The suspension was filtered through two layers of Miracloth, and the chloroplasts pelleted by centrifugation at 400*g* for 2 min. The chloroplasts were washed by resuspension in the extraction solution and repelleted. The thylakoids were isolated by rupturing the chloroplasts in extraction solution containing only 100 mM sorbitol; the osmotic strength was then adjusted to 400 mM sorbitol to approximate conditions *in vivo*, and the thylakoids pelleted by centrifugation at 3000*g* for 3 min.

The isolated thylakoids were tested for whole chain electron transport activity as described previously (21). O_2 evolution was measured polarographically with a Rank O_2 electrode at 25°C with 1000 μE PAR m^{-2} s^{-1} in the presence of 2.5 mM NH_4Cl, 10 mM glyceraldehyde, 1.5 mM $K_3Fe(CN)_6$, 400 mM sorbitol, 30 mM

[1] Abbreviations: *P*, rate of photosynthetic CO_2 uptake; C_i, intercellular CO_2 concentration; Γ, CO_2 compensation point; RuBP, ribulose 1,5-bisphosphate; RuBPCase, ribulose 1,5-bisphosphate carboxylase; P_{max}, maximal rate of photosynthesis.

Na pyrophosphate (pH 7.6), and 50 μg Chl/3 ml cuvette.

RuBPCase Assays. Assays of RuBPCase activity were carried out according to Perchorowicz *et al.* (23). A known volume of leaf plugs (approximately 0.5 g) were ground in a chilled glass homogenizer with 2 ml of extraction buffer (50 mM Hepes-KOH [pH 7.0], 10 mM $NaHCO_3$, 5 mM $MgSO_4$, 1 mM EDTA, 10 mM DTT, 10 mM Na ascorbate, and 1% (w/v) PVP-40 at 0°C). The resulting homogenate was filtered through two layers of Miracloth, and 20 μl added to an assay solution of 80 mM Tris-HCl (pH 8.1), 16 mM $MgCl_2$, 1 mM DTT, 20 mM $NaH^{14}CO_3$ (0.5 mCi/mmol) resulting in a final volume of 480 μl. The mixture was incubated at 29°C for 10 min to activate the RuBPCase, then 20 μl of 20 mM RuBP was added to initiate the reaction. The reaction was stopped after 1 min by the addition of 0.5 ml of 6 N acetic acid. This assay measured the total inducible activity of the enzyme.

The percentage of 'active' RuBPCase (*i.e.* the activity of the enzyme rapidly extracted and assayed without preincubation with CO_2 and Mg^{2+}) was determined according Perchorowicz *et al.* (23). The assays were performed on leaves of normal (iron-sufficient) plants. Leaves were irradiated for 1 h under a range of light intensities from 100 to 1500 μE m^{-2} s^{-1}, then twenty plugs were removed directly from the attached leaves and placed in 2 ml of ice-cold extraction buffer as quickly as possible (within 30 s), and RuBPCase extracted as before. Total inducible RuBPCase activity was determined as above. The initial RuBPCase activity was determined by adding 20 μl of extract to the assay solution that contained the appropriate amount of RuBP, and $^{14}CO_2$ fixation was allowed to occur for 1 min.

A liquid scintillation counter was used to determine ^{14}C fixation in all of these experiments. Chl was determined using leaf plugs as described previously (1).

RESULTS

The characteristic changes in photosynthetic rate, P/area, with intercellular CO_2 concentration, C_i, are shown for a leaf at two O_2 concentrations in Figure 1. The shape of the P/C_i curve at 21% O_2 (Fig. 1A) is the same as has been found by other researchers (9, 17, 30). The increase in P/area with C_i was linear over the low CO_2 concentration range. At about 225 μl l^{-1} CO_2, the slope of the curve begins to decrease. At this CO_2 concentration, referred to by Farquhar *et al.* (13) as the inflection point, P/area increased more slowly with increase in C_i. The photosynthetic rate reached a maximum value (P_{max}) at about 650 μl l^{-1} CO_2 (internal).

At 1% O_2 (Fig. 1B), the initial slope was greater than that at 21% O_2. The inflection point was lower, about 125 μl l^{-1} CO_2. The P/C_i curve under low O_2 exhibited a more abrupt transition between the two phases than under 21% O_2. P_{max}/area was attained at lower C_i values (about 400 μl l^{-1} CO_2) than at 21% O_2 but the P_{max}/area values were the same at the two O_2 concentrations.

When the rate of supply of photochemical energy was reduced by decreasing irradiance, the initial slope and P_{max} values of the P/C_i curve decreased both at 21% O_2 and 1% O_2 (Fig. 2). Most of the decrease in initial slope and in P_{max} occurred from 1000 to 100 μE PAR m^{-2} s^{-1}.

An alternative procedure for altering the rate of supply of photochemical energy is to selectively reduce photosynthetic electron transport capacity by depriving plants of Fe (27). As indicated by the data shown in Figure 3, the rate of light-saturated electron transport (water to ferricyanide) decreased linearly with Chl content while maximum extractable RuBPCase activity per area showed no significant change. When P/C_i curves were measured on leaves of different Chl content (used here as an index of the total amount of light harvesting and electron transport components; see 28), initial slope and P_{max} each decreased linearly with Chl content at both 1% and 21% O_2 (Fig. 4). We conclude from these data (Figs. 2 and 4) that the initial slope of the P/C_i curves was influenced by the rate of supply of photochemical energy, whether varied by irradiance level or electron transport capacity.

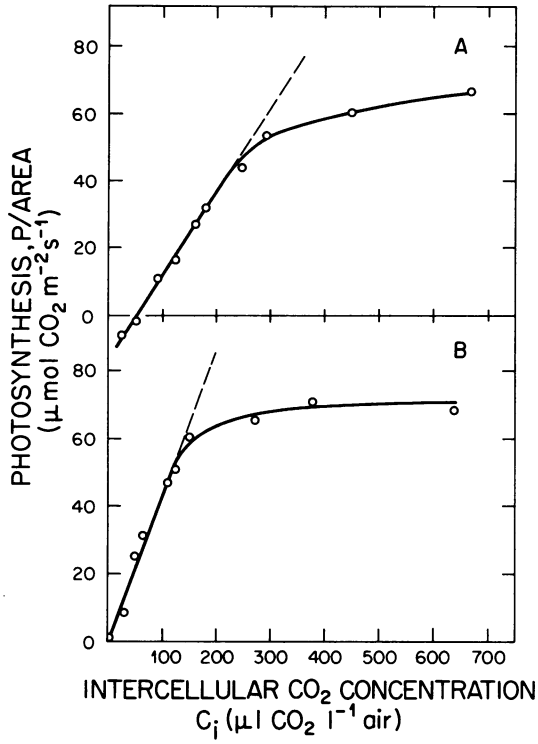

FIG. 1. The relationship of P/area to intercellular CO_2 concentration at O_2 concentration levels of 21% (A) and 1% (B). Irradiance of 3000 μE m^{-2} s^{-1} was used. Leaf Chl content: 0.693 mM Chl m^{-2}.

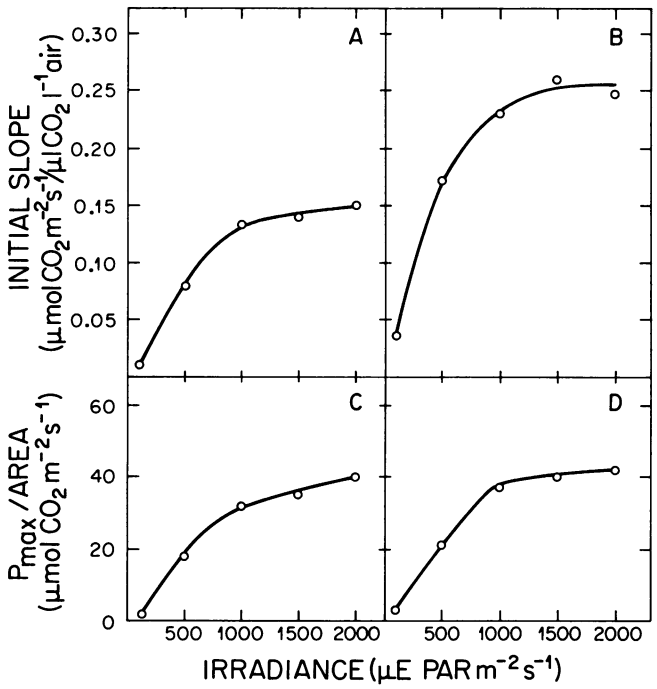

FIG. 2. Initial slope and P_{max}/area of P/C_i curves measured at different constant irradiances and at two different O_2 concentrations (A and C, 21% O_2; B and D, 1% O_2). Leaf Chl content: 0.546 ± 0.073 mM Chl m^{-2}.

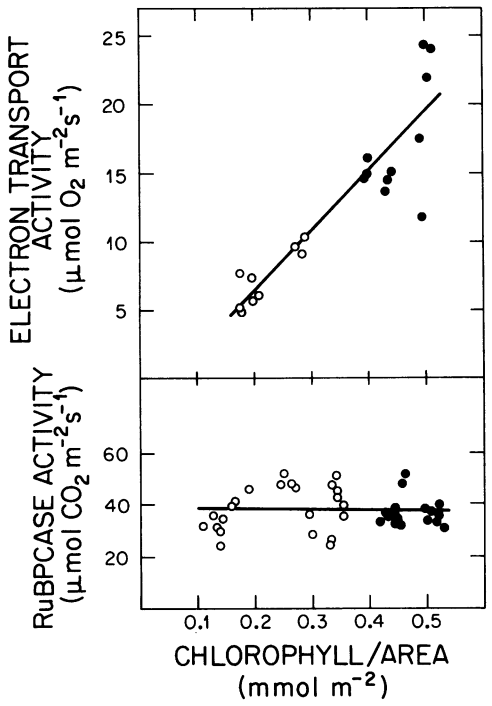

FIG. 3. Photosynthetic electron transport activity and RuBPCase activity in Fe-deficient and Fe-sufficient plants. Electron transport activity was measured from $H_2O \rightarrow FeCN$, monitoring O_2 evolution with an O_2 electrode. RuBPCase activity represents total extractable activity (*i.e.* fully induced). (●), Control plants (iron sufficient); (○), iron-deficient plants. (Electron transport: $y = 43.65x - 2.10$, $r = 0.913$; RuBPCase: $y = -3.06x + 39.4$, $r = -0.047$)

One possible mechanism whereby the electron transport system could alter the initial slope is by varying the level of activation of RuBPCase. This was investigated by determining the ratio of initial extractable activity to total inducible activity of RuBPCase from attached leaves irradiated at different light intensities (Fig. 5). At 100 $\mu E\ m^{-2}\ s^{-1}$, RuBPCase appeared to be only 25% activated; with increase in irradiance to 1500 $\mu E\ m^{-2}\ s^{-1}$, the ratio of initial to total activity increased to 90%. These data suggested that variation in photochemical energy supply may be mediated, at least in part, through the level of activation of RuBPCase.

DISCUSSION

Farquhar *et al.* (13) centered their conceptual model of photosynthesis on the kinetics of RuBPCase. The biochemical basis of this approach was formulated from the mechanism of ordered binding first proposed by Laing and Christeller (19). In this scheme, RuBPCase combines first with RuBP to give an enzyme-RuBP complex which subsequently binds with CO_2 or O_2:

$$E_A \overset{R}{\rightleftharpoons} E_AR \overset{C}{\rightleftharpoons} E_ARC \rightarrow E_A + 2P \qquad E_AR \overset{O}{\rightleftharpoons} E_ARO \rightarrow E_A + P + G \qquad (1)$$

where E_A represents the activated enzyme-CO_2-Mg^{2+} complex (22); R, RuBP; O, O_2; C, CO_2; P, 3-P-glycerate; and G, P-glycolate (11). From this, Farquhar formulates the following general case model:

$$A = \frac{CM}{CM + K_{cm}} \frac{V_{cmax}(C - \Gamma_*)}{C + K_c(1 + O/K_o)} \frac{R}{R + K_r''} - R_d \qquad (2)$$

where A represents P/area; K_{cm}, the affinity constants for CO_2 and Mg^{2+}; M, Mg^{2+}; Γ_*, CO_2 compensation concentration; K_c, K_o, K_r, the Michaelis constants for CO_2, O_2, and RuBP; and R_d, 'day' respiration (for more complete description and derivation of these terms, see 29; also, note that $CM/(CM + K_{cm})$ represents the degree of activation of RuBPCase).

Farquhar *et al.* (13) assume that the concentration of RuBP exceeds the concentration of active sites, and, that RuBPCase is fully activated. Thus, in equation 2, $R/(R + K_r)$ and $CM/(CM + K_{cm})$ each become equal to unity so that A becomes dependent on the remaining terms. One important consequence of these assumptions is that the initial slope of the P/C_i curve would therefore be independent of the supply of photochemical energy. This was in fact found experimentally by Collatz (9) and by von

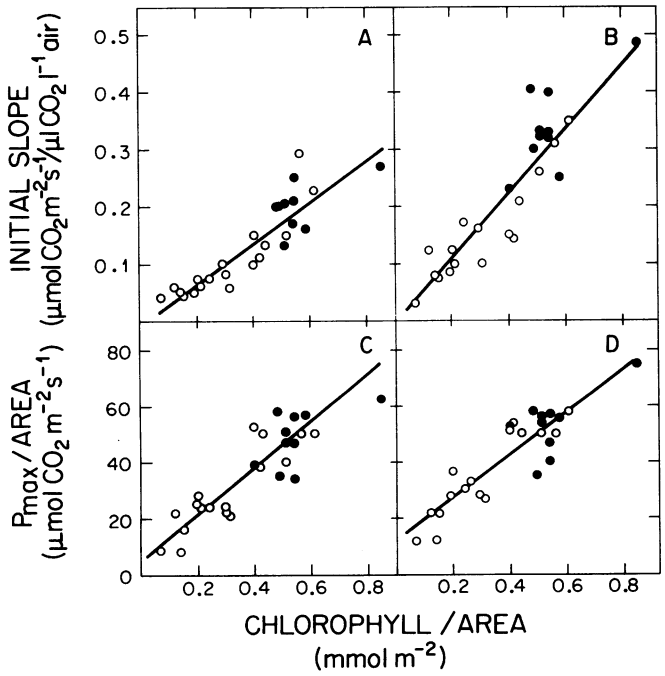

FIG. 4. Initial slope and P_{max}/area of P/C_i curves as a function of leaf Chl content. A and C, 21% O_2; B and D, 1% O_2. (●), Control plants (iron sufficient); (○), iron-deficient plants.

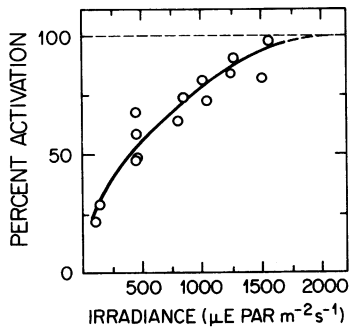

FIG. 5. Percentage of activated RuBPCase as a function of light intensity on leaf surface. The percentage was calculated from the ratio of initial activity *versus* fully inducible activity. Only control plants were used for this experiment.

Caemmerer and Farquhar (30).

In the present work, we obtained the opposite result, *i.e.* the initial slope of the P/C_i curve did change in response to variation in the supply of photochemical energy, whether it was varied by changing light intensity or photosynthetic electron transport capacity. This suggests a different view of photosynthetic limitation, *i.e.* that photosynthetic rate may be colimited by photochemical energy supply and CO_2 concentration simultaneously, even at very low and limiting C_i values.

Other researchers have reported differences in initial slope with photochemical energy supply as varied by changes in irradiance. Samish and Koller (25) concluded that the rate of photosynthesis at low C_i values should be affected by the light intensity. Hew *et al.* (15) reported that the rate of apparent photosynthesis at low CO_2 was increased if the light intensity were increased. Augustine *et al.* (2) found that carboxylation efficiency (measured at low C_i) increased with increasing light intensity. Bradford *et al.* (6) observed differences in initial slope with changes in light intensity, though they only measured the P/C_i curves at high and low light.

How might colimitation between photochemical energy supply and CO_2 concentration be mediated in biochemical terms? The Farquhar model assumes that the supply of photochemical energy affects P via the supply of RuBP and that the total (free and bound) RuBP concentration at low values of C_i is greater than the concentration of active sites of RuBPCase. Thus, the formation of the enzyme-RuBP complex (ER) is occurring at its maximal velocity and P is determined solely by the rates of carboxylation and oxygenation of the ER complex. For colimitation to occur on the other hand, photochemical energy supply could influence either the level of activation of RuBPCase or the concentration of RuBP. Either way, a reduction in photochemical energy supply would lead to a decrease in the rate of ER formation and, with it, P, even at low values of C_i.

What evidence is there that the supply of photochemical energy affects the level of activation of RuBPCase? Studies have shown that carboxylase may be regulated by pH and Mg^{2+} concentration (5, 22). Both of these factors may be influenced by the activity of the electron transport system since the latter appears to control the movement of H^+ and Mg^{2+} between the thylakoids and the stroma. A product of the photochemical reactions may also regulate RuBPCase activity through direct enzyme activation. NADPH has been reported to potentiate RuBPCase activation (8). In addition, Calvin cycle intermediates may bind to and alter the activity of RuBPCase (3, 7, 8, 14). Our results suggest that RuBPCase activation may be regulated by the level of irradiance with the enzyme becoming increasingly less active as irradiance decreases from 1500 to 100 $\mu E\ m^{-2}\ s^{-1}$. Similar results were obtained by Perchorowicz *et al.* (24). Sicher and Jensen, (26) who found CO_2 fixation in spinach decreased under low light while RuBP concentration remained the same, suggest that light mediates the level of activation of RuBP carboxylase so that the concentrations of RuBP and other Calvin cycle intermediates remain constant.

The concentration of RuBP in the chloroplast stroma, especially in relation to the concentration of RuBPCase active sites, is obviously of critical importance in determining how photochemical energy supply influences photosynthesis. Farquhar *et al.* (13) assume that the initial slope of the P/C_i curve is RuBP-saturated and the plateau phase RuBP-limited. The concentration of RuBP relative to the concentration of active sites is difficult to determine. Hitz and Stewart (16) found that the concentration of RuBP in soybean was less than that of RuBPCase active sites, even under high light and low CO_2 concentrations; however, they compared their RuBP values to the total number of available sites and did not determine how many of these sites were active. Collatz (10) reported that RuBP concentrations in spinach remained constant and above the concentration of active sites even under diminishing light. Perchorowicz *et al.* (23) found in wheat that RuBP levels remained above saturation at irradiances greater than 225 $\mu E\ m^{-2}\ s^{-1}$. Sicher and Jensen (26) obtained reductions in RuBP in spinach under some conditions but not others.

Preliminary results with sugar beet in our laboratory indicate that the levels of RuBP remain constant or even increase with diminishing light. This is consistent with the data presented above (Fig. 5) and suggests that sugar beet respond to low light intensities by diminishing the level of activation of RuBPCase in order to maintain RuBP concentrations at a high level. The data also suggest that the decrease in initial slope which we observed with reduced photochemical energy supply may well be due to a diminished number of available catalytic sites; thus, the colimitation of photosynthetic rate at low C_i values by photochemical energy supply may not be due to a direct effect on RuBP production, but may be manifested indirectly via activation of RuBPCase.

All of the models proposed above to explain the changes in P/C_i curves in terms of biochemical characteristics are based on the Laing and Christeller model of ordered binding. There is a substantial amount of evidence for this model (19, 22). However, it is only fair to point out that there is some evidence that RuBP may bind randomly to the enzyme (4). Furthermore, Laing and Christeller (19) have postulated that partially activated RuBPCase may also react with the substrates, CO_2, O_2, and RuBP, and carry out carboxylation or oxygenation. Thus the reaction may not be as proposed in equation 1 but may instead be a matrix of reactions with many different K_m and V_{max} values for each substrate.

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