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Limiting Factors in Photosynthesis

IV. IRON STRESS-MEDIATED CHANGES IN LIGHT-HARVESTING AND ELECTRON TRANSPORT CAPACITY AND ITS EFFECTS ON PHOTOSYNTHESIS *IN VIVO*

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ABSTRACT

Using iron stress to reduce the total amount of light-harvesting and electron transport components per unit leaf area, the influence of light-harvesting and electron transport capacity on photosynthesis in sugar beet (*Beta vulgaris* L. cv F58-554H1) leaves was explored by monitoring net CO_2 exchange rate (*P*) in relation to changes in the content of Chl.

In most light/CO_2 environments, and especially those with high light (≥1000 microeinsteins photosynthetically active radiation per square meter per second) and high CO_2 (≥300 microliters CO_2 per liter air), *P* per area was positively correlated with changes in Chl (*a* + *b*) content (used here as an index of the total amount of light-harvesting and electron transport components). This positive correlation of *P* per area with Chl per area was obtained not only with Fe-deficient plants, but also over the normal range of variation in Chl contents found in healthy, Fe-sufficient plants. For example, light-saturated *P* per area at an ambient CO_2 concentration close to normal atmospheric levels (300 microliters CO_2 per liter air) increased by 36% with increase in Chl over the normal range, *i.e.* from 40 to 65 micrograms Chl per square centimeter. Iron deficiency-mediated changes in Chl content did not affect dark respiration rate or the CO_2 compensation point. The results suggest that *P* per area of sugar beet may be colimited by light-harvesting and electron transport capacity (per leaf area) even when CO_2 is limiting photosynthesis as occurs under field conditions.

Iron stress has been shown to diminish the thylakoid content of sugar beet chloroplasts (15, 18). This leads to concomitant reductions in Chl *a*, Chl *b*, P_{700}, and Cyt *f* contents (18) and to a corresponding reduction in photosynthetic electron transport capacity in chloroplasts (22). In contrast, Fe stress has little or no effect on the extractable activities of Calvin cycle enzymes (19, 22) and does not affect cell or chloroplast number/area, cell volume, soluble leaf protein, leaf thickness, leaf fresh weight per area, and other leaf attributes (21, 22). Thus, as proposed earlier (18, 19, 21, 22), Fe stress provides an experimental means for studying the quantitative influence of light-harvesting and electron transport capacity on photosynthesis *in vivo*.

The objective of the present work was to explore the effects of Fe deficiency-mediated reduction in light-harvesting and electron transport capacity on the photosynthesis of sugar beets in a range of light/CO_2 environments, and in particular, to determine whether decrease in photochemical capacity significantly reduced photosynthesis in environments approximating those found under field conditions where CO_2 is known to limit photosynthesis.

MATERIALS AND METHODS

Procedure for Inducing Fe Deficiency Chlorosis. Sugar beets (*Beta vulgaris* L. cv F58-554H1) were cultured hydroponically at 25°C and illuminated at 800 μE PAR m^{-1} s^{-1} over a 16-h day. After germination, the plants were cultured for 2 weeks in vermiculite irrigated with half-Hoagland solution. They were then transplanted into a culture solution containing (in mM): 2.5 $Ca(NO_3)_2$, 1.0 KH_2PO_4, 2.5 KNO_3, 1.0 $MgSO_4$, and 0.15 NaCl and (in μM) 23.1 B, 4.6 Mn, 0.38 Zn, 0.16 Cu, 0.052 Mo, and 8.95 Fe (ferric-sodium EDTA complex). After 2 weeks, the plants were transferred to solutions with the same composition as above, except for Fe, which was withheld; 2 M NaOH and solid $CaCO_3$ were added to raise the pH to 8.5 (to precipitate any Fe present in root cell walls). Iron deficiency chlorosis usually followed within 3 d and plants were discarded after 8 d.

The degree of chlorosis in a given leaf was determined by measuring Chl (*a* + *b*) /area (23). P_{700} and Cyt *f* were determined concomitantly with Chl *a* and Chl *b* in some leaves, according to the method of Spiller and Terry (18), to check that the amounts of P_{700} and Cyt *f* were related to Chl (*a* + *b*) content according to the relationships shown in Figures 1 and 2 of Spiller and Terry (18).

Young leaves about 150 to 200 cm^2 in area were chosen for gas exchange analysis because these rapidly growing leaves exhibit very high rates of photosynthesis.

Experiment 1. P[1]/area of individual attached leaves was determined for a range of irradiances at each of four ambient CO_2 concentrations: 150, 300, 600, and 1000 μl L^{-1} air. The leaf was inserted in the leaf chamber of an open flow gas exchange apparatus as described previously (20). The ambient CO_2 concentration was adjusted to one of the above levels (±1%) and leaf temperature was maintained at 30 ± 0.5°C.

With leaves of high Chl content (>30 μg cm^{-2}), CO_2 uptake, H_2O vapor efflux, and leaf temperature were measured for 1 h at each of the following irradiances: 100, 500, 1000, 2000, and 3000 μE PAR m^{-2} s^{-1}; with leaves of low Chl content (<30 μg cm^{-2}), the irradiances were 100, 300, 500, 1000, 1500, and 2000 μE PAR m^{-2} s^{-1}.

Leaf (mainly stomatal) conductance to CO_2 (g_{CO_2}) was determined following the procedure for measurement of leaf diffusion resistance to CO_2 (r_1) and g_{CO_2} calculated as $1/r_1$ (see Equation 2, Ref. 24). Intercellular CO_2 concentration was calculated as reported earlier (24).

Experiment 2. In the second series of experiments, plants were removed from the growth chamber and an attached leaf was inserted in the leaf chamber which was then darkened with

[1] Abbreviations: *P*, net CO_2 exchange rate; R_D, rate of respiratory evolution of CO_2 in darkness; g_{CO_2}, leaf CO_2 conductance; C_i, intercellular CO_2 concentration; Γ, CO_2 compensation point; RuBP, ribulose 1,5-bisphosphate; RuBPCase, ribulose 1,5-bisphosphate carboxylase (EC 4.1.1.39); FBPase, fructose 1,6-bisphosphatase (EC 3.1.3.11); GPDHase, NADP-glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.13); PRKase, ribulose-5-phosphate kinase (EC 2.7.1.19).

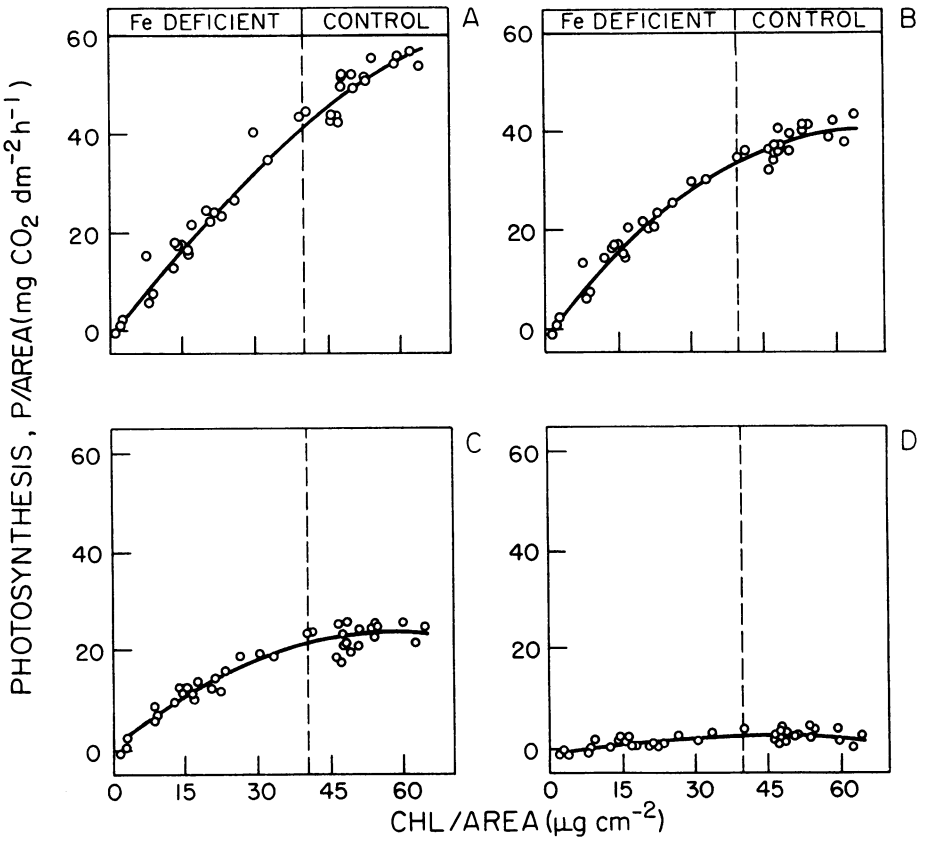

FIG. 1. The relationship of P/area with Chl content at different irradiances. P/area was measured at an ambient CO_2 concentration of 300 μl L^{-1} CO_2. A, P/area at saturating irradiance; B, P/area at 1000 μE PAR m^{-2} s^{-1}; C, P/area at 500 μE PAR m^{-2} s^{-1}; D, P/area at 100 μE PAR m^{-2} s^{-1}. Curves were fitted by polynomial regression, *e.g.* the regression for A is $y = -2.07 + 1.37x - 0.0072x^2$.

Table I. *P_{700} and Cyt f Contents and Their Relation to Chl in Leaves of Different Chl Contents*

Values based on regressions obtained by Spiller and Terry (18), *i.e.* for P_{700}/area, $y = 1.81x - 9.82$ ($r = 0.97$); for Cyt f per area, $y = 1.80x - 7.35$ ($r = 0.96$); for Chl/P_{700}, $y = -3.15x + 598$ ($r = -0.70$); and for Chl/Cyt f, $y = -1.41x + 496$ ($r = -0.32$).

	Chl/Area	P_{700}	Chl/P_{700}	Cyt f	Chl/Cyt f
	$\mu g\ cm^2$	10^{12} molecules cm^{-2}		10^{12} molecules cm^{-2}	
Control	65	108	393	110	404
	40	62.6	474	64.7	440
Fe deficient	35	53.5	488	55.7	447
	25	35.4	519	37.7	461
	15	17.3	551	19.7	475

aluminum foil for 16 h. The following day, R_D was determined by measuring the rate of CO_2 efflux per unit leaf area at 30 ± 0.5°C. The leaf was irradiated at the saturating irradiance of 2000 μE PAR m^{-2} s^{-1} (unless the leaves were chlorotic, in which case 1000 μE PAR m^{-2} s^{-1} was used) and P/area measured at decreasing ambient CO_2 concentrations of 200, 150, 100, 50, and 0 μl L^{-1} air. The CO_2 compensation concentration (Γ) was calculated from the linear regression of P/area with C_i.

RESULTS

Photosynthesis-Chl Relationships at Different Irradiances. The relationships of P/area (measured at an ambient CO_2 concentration of 300 μl L^{-1}) with Chl content at different irradiances are shown in Figure 1. Chl content is considered here to reflect changes in the total amount of light-harvesting and electron transport components (see "Discussion"); its specific relationships with P_{700} and Cyt f contents are shown in Table I. The values shown in Table I are based on data obtained by Spiller and Terry (18) at the same time and under the same conditions as reported in the present work. Part of the change in Chl content was achieved using Fe deficiency (those Chl contents lower than 40

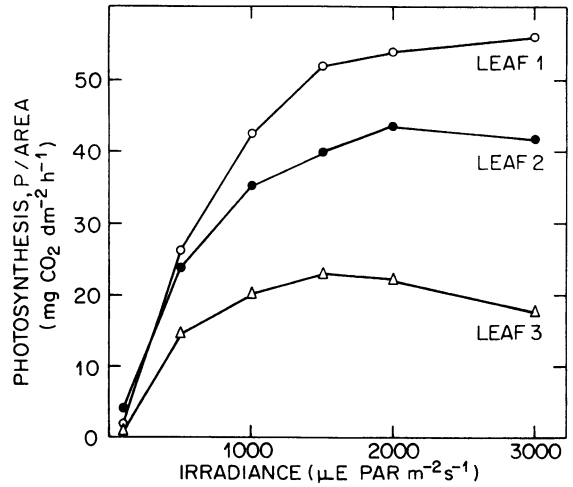

FIG. 2. The relationship of P/area with irradiance for leaves with different Chl contents. Leaves 1 and 2 were from Fe-sufficient control plants and leaf 3 from an Fe-deficient plant. The Chl contents of leaves 1, 2, and 3 were 60, 40.2, and 21.3 $\mu g\ cm^{-2}$, respectively. P/area was measured at an ambient CO_2 concentration of 300 μl L^{-1}.

$\mu g\ cm^{-2}$) and part of the change in Chl content resulted from normal variation in Fe-sufficient, control plants (40 to 65 μg Chl cm^{-2}).

Light-saturated *P*/area increased almost linearly with increase in Chl content (Fig. 1A). There was no abrupt transition between the data obtained with Fe-deficient plants and the data obtained with control plants, *i.e.* the curve of the relationship with Chl content appeared to continue smoothly through both sets of data. *P*/area increased over 10-fold (from 3 to 41 mg CO_2 dm^{-2} h^{-1}) with a 10-fold increase in Chl over the Fe-deficient range (from 4 to 40 $\mu g\ cm^{-2}$). While the increase in *P*/area with Chl content over the Fe-sufficient range was less dramatic, it was significant; *P*/area increased 36% with increase in Chl from 40 to 65 $\mu g\ cm^{-2}$.

As the amount of Chl in leaves increased, there was an increase in the light intensity required for saturation. This is illustrated in Figure 2, which shows the light saturation curves of photosynthesis for three specific leaves (Fig. 2). Leaves 1 and 2 were obtained from Fe-sufficient control plants and leaf 3 from an Fe-deficient plant. The increase in light-saturated *P*/area which occurred in leaf 2 or leaf 1 compared to leaf 3 was not due to an increase in *P*/Chl; light-saturated *P*/Chl in leaves 1, 2, and 3 were 211, 247, and 241 $\mu mol\ CO_2\ mg^{-1}$ Chl h^{-1}, respectively.

At an irradiance of 1000 $\mu E\ PAR\ m^{-2}\ s^{-1}$, the initial slope of the relationship of *P*/area with Chl/area (Fig. 1*B*) is the same as that shown in Figure 1A. This is because *P*/area in leaves with very low Chl contents (<10 $\mu g\ cm^{-2}$) was light saturated at 1000 $\mu E\ PAR\ m^{-2}\ s^{-1}$. As Chl content increased, this irradiance level was insufficient to saturate photosynthesis: nevertheless, these light-limited *P*/area values continued to increase with increase in Chl content. At 100 and 500 $\mu E\ PAR\ m^{-2}\ s^{-1}$ (Fig. 1, D and C, respectively), the irradiances were insufficient to saturate *P*/area and the initial slopes were less. Figure 1 shows that *P*/area increased most with increase in Chl content at saturating irradiances, but that there was still a substantial increase in *P*/area even under light-limited conditions (*e.g.* at 500 $\mu E\ PAR\ m^{-2}\ s^{-1}$).

Photosynthesis-Chl Relationships at Different Ambient CO_2 Concentrations. The influence of ambient CO_2 concentration on the relationship of light-saturated *P*/area with Chl is shown in Figure 3. Light-saturated *P*/area reached its maximum value at about 1000 $\mu l\ L^{-1}$ CO_2. At this concentration, *P*/area increased almost linearly with increase in Chl content (Fig. 3A). With each successive lowering of the CO_2 concentration (to 600, 300, and 150 $\mu l\ L^{-1}$ [Fig. 3, B, C, and D, respectively]), the slope of the curve diminished. At the lowest ambient CO_2 level (150 $\mu l\ L^{-1}$ CO_2, Fig. 3D), *P*/area increased with Chl over the initial part of the range, and then leveled off. This suggests that ambient CO_2 at 150 $\mu l\ L^{-1}$ so strongly limited photosynthesis that there was no further response to an increase in light-harvesting and electron transport components over the upper part of the Chl range.

Stomatal Conductance. The data presented above show that *P*/area decreased significantly with decreases in Chl content over a wide range of light/CO_2 environments. An important question to consider is to what extent was *P*/area diminished due to Fe deficiency-mediated reductions in stomatal conductance? Measurement of g_{CO_2} (which was mainly stomatal conductance) indicated a linear decrease in g_{CO_2} with decrease in Chl content in some environments (see Fig. 4 and Table II). However, the reduction in g_{CO_2} with decreased Chl presumably had only small negative effects on *P*/area because C_i was constant or increased with decrease in Chl (Fig. 4).

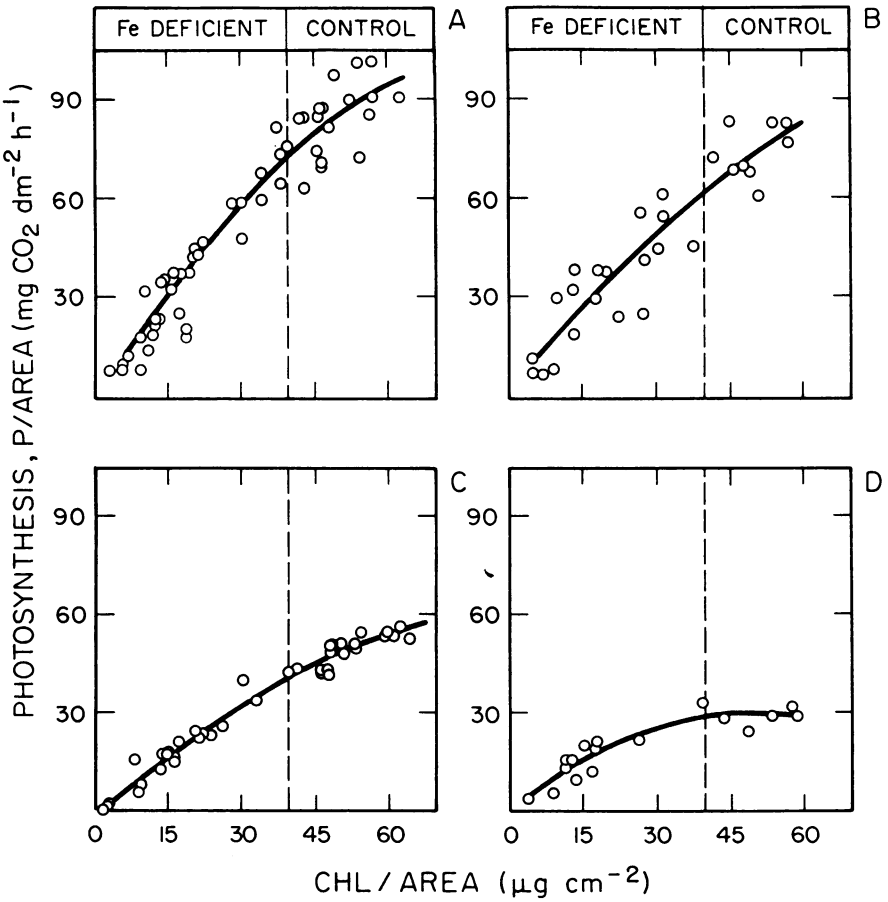

FIG. 3. The relationship of light-saturated *P*/area with Chl content at different ambie O_2 concentrations. A, *P*/area at 1000 $\mu l\ L^{-1}$ CO_2; B, *P*/area at 600 $\mu l\ L^{-1}$ CO_2; C, *P*/area at 300 $\mu l\ L^{-1}$ CO_2; D, *P*/area at 150 $\mu l\ L^{-1}$ CO_2. Curves were fitted by polynomial regression.

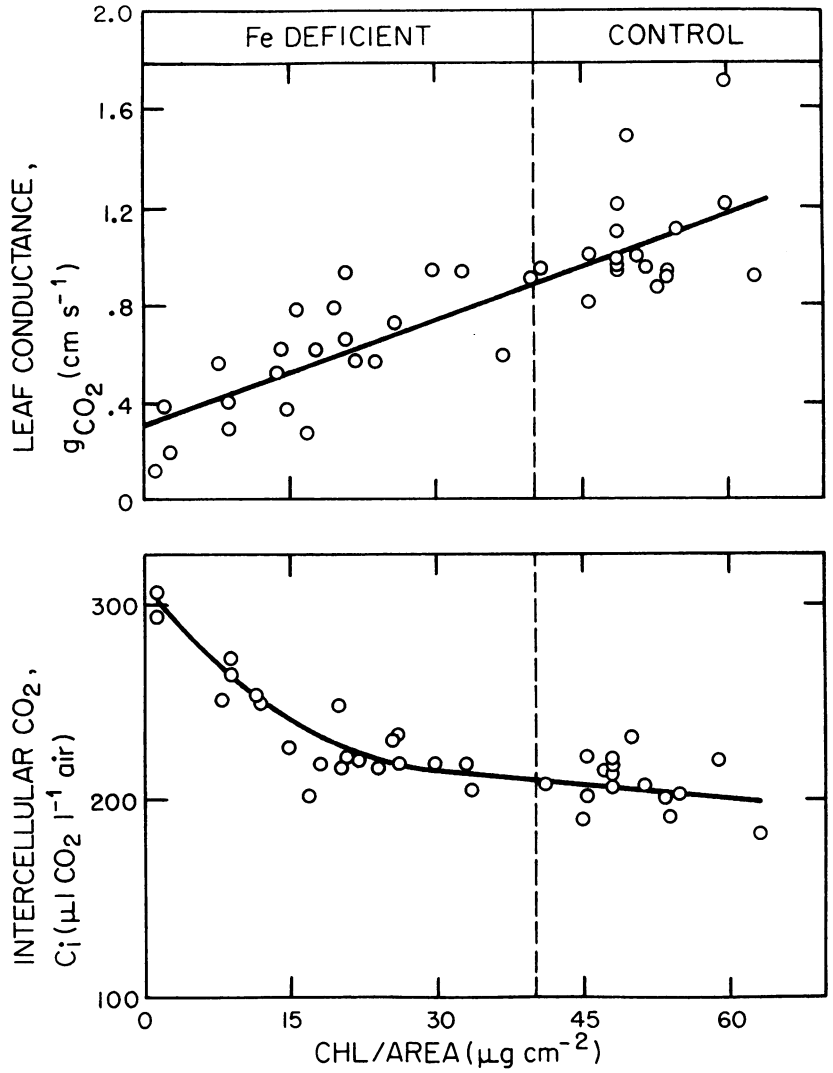

FIG. 4. Changes in leaf conductance (g_{CO_2}) and intercellular CO_2 concentration (C_i) with variation in Chl content. The data are for light-saturated leaves photosynthesizing at an ambient CO_2 concentration of 300 µl L^{-1}.

Respiratory Attributes. Iron deficiency-mediated reductions in Chl did not reduce R_D (Fig. 5). Variation in Chl content also had no significant effect on the CO_2 compensation point (Fig. 5). This suggests that the ratio of the rates of carboxylation to oxygenation for RuBPCase/oxygenase did not change as a result of Fe deficiency-mediated variation in Chl.

DISCUSSION

The data presented above suggest that *P*/area of sugarbeets may be colimited by light-harvesting and electron transport capacity in addition to other factors (*e.g.* CO_2 supply) over a wide range of light/CO_2 environments. This view is predicated on two main assumptions: (a) that the changes in Chl content measured here correspond to parallel changes in the amount of the total light-harvesting and electron transport components (per area), and (b) that Fe deficiency effects on photosynthesis are specifically mediated via changes in the light-harvesting and electron transport apparatus. The validity of these two assumptions is considered below.

That changes in Chl content signal changes in the total amount of the light-harvesting and electron transport apparatus is supported by several different types of evidence. Spiller and Terry (18) and Platt-Aloia *et al.* (15) showed that Fe deficiency results in a substantial reduction in thylakoids within the chloroplasts. Furthermore, the decrease in Chl content is accompanied by a proportional decrease in P_{700} and Cyt *f* (18), and in Chl-protein complexes (12). The first stable electron acceptor of PSII, Q, is also reduced, although not quite as much as P_{700} (13). As discussed earlier (22), the reduction in light-harvesting and electron transport components results in a much greater decrease in photosynthetic electron transport activity than in the absorptance of white light. Thus, the decreases in *P*/area which occurred with decrease in Chl content are considered to be more related to the reduction in the number of electron carriers and reaction centers (*i.e.* electron transport chains) than to the decrease in light absorption which accompanied the drop in Chl content *per se* (this is especially true at high irradiances).

That Fe deficiency influences photosynthesis via changes in the light-harvesting and electron transport apparatus and not by changes in other parts of the photosynthetic apparatus is indicated by the following: (a) electron microscopy of sugar beet leaf cells shows that the effects of Fe deficiency are confined to the thylakoid system of chloroplasts; the mitochondria, microbodies, ER, and other aspects of cell structure appear to be unaltered (15); (b) Fe deficiency does not appear to affect other parameters of leaf structure, *e.g.* leaf thickness, fresh weight per area, number of cells or chloroplasts per area, and cell volume, and only slightly reduces

Table II. *Changes in g_{CO_2} with Chl Content at Different Levels of Irradiance and CO_2 Supply*

Ambient CO_2 concentration	Chl/Area	g_{CO_2}[a] Irradiance[b]				
		100	300	500	1000	Saturation
$\mu l\ L^{-1}$	$\mu g\ cm^{-2}$			$cm\ s^{-1}$		
150	5		0.81	1.00	1.24	1.52
	50		0.56	0.79	1.30	1.92
300	5	0.16		0.33	0.36	0.36
	50	0.29		0.57[c]	0.81[c]	1.06[c]
600	5			0.23	0.32	0.35
	50	1.01		0.27	0.42	0.65[d]
1000	5	0.21	0.23	0.23	0.29	0.25
	50	0.10	0.20	0.23	0.41	0.70[c]

[a] Values obtained from linear regressions of g_{CO_2} with Chl/area.
[b] Units are μE PAR $m^{-2}\ s^{-1}$.
[c] Significant at P = 0.001.
[d] Significant at P = 0.05.

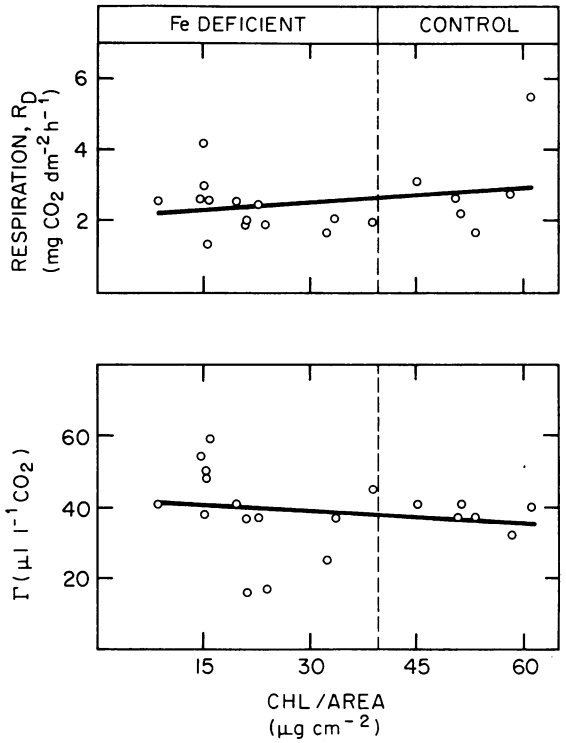

FIG. 5. Changes in dark respiration (R_D) and CO_2 compensation point (Γ) with variation in Chl content (see Experiment 2 of "Materials and Methods" for measurement procedure).

leaf growth rate (21, 22); (c) the extractable activities of several major Calvin cycle enzymes were either not affected by Fe deficiency (GPDHase, PRKase, FBPase, [19]) or reduced slightly (RuBPCase, [22]); and (d) the data of the present work shows that Fe deficiency probably did not influence photosynthetic rate via changes in stomatal conductance, dark respiration or CO_2 compensation point.

The present work supports the view proposed by Lilley and Walker (11) and Farquhar *et al.* (7) that photosynthesis at high ambient CO_2 concentrations may be limited by photosynthetic electron transport capacity. *P*/area was almost linearly related with Chl content at ambient CO_2 concentrations of 600 and 1000 $\mu l\ L^{-1}$ CO_2 (Fig. 3). Furthermore, if one recalculates the data on a per Chl basis, *P*/Chl was constant over almost the entire range of Chl contents. This suggests that Fe deficiency reduced light-saturated *P*/area by reducing the per area amounts of reaction centers and electron carriers without otherwise impairing the efficiency of the photosynthetic apparatus (or increasing the antenna size per reaction center; see Ref. (18).

Unlike the situation at high CO_2 levels, it is thought that at low ambient CO_2 concentrations CO_2 assimilation follows the kinetics of the RuBP-saturated rate of carboxylase and is relatively independent of the photochemical reactions (5, 7). This may well be true for *P*/area at 150 $\mu l\ L^{-1}$ CO_2 since *P*/area was independent of Chl content over the normal range (*i.e.* Fe-sufficient plants). However, the data for *P*/area at 300 $\mu l\ L^{-1}$ CO_2 indicated a strong dependence of light-saturated photosynthesis on Chl content throughout the range including Fe-sufficient control plants (Fig. 1A). Thus, *P*/area appeared to be colimited by both ambient CO_2 and photochemical capacity because an increase in either factor independent of the other resulted in an increase in *P*/area. The fact that light-saturated *P*/area at 300 $\mu l\ L^{-1}$ CO_2 increased by 36% with increase in Chl over the normal range, *i.e.* from 40 to 65 μg Chl cm^{-2}, is especially interesting because no Fe deficiency was involved over this part of the Chl range and because there was also no detectable change in the extractable activities of RuBPCase, FBPase, GPDHase, and RPKase, indicating that the increase in *P*/area was not due to increases in the amounts of these enzymes.

The increase in *P*/area with increase in Chl content at light saturation can be attributed to an increase in the photochemical conversion of absorbed light rather than to an increase in light absorption (as discussed above). At limiting irradiances, on the other hand, one might expect that an increase in Chl content might enhance *P*/area by increasing the quantity of light (photon flux density) absorbed. However, even at limiting irradiances, the improvement in light absorption may be less important than the improvement in photochemical conversion. For example, *P*/area at the limiting irradiance of 500 μE PAR $m^{-2}\ s^{-1}$ (Fig. 1C) increased 6-fold (from 4 to 24 mg CO_2 $dm^{-2}\ h^{-1}$) with increase in Chl content from 5 to 60 $\mu g\ cm^{-2}$. Absorptance of white light, however, increased much less, *i.e.* from 51 to 81% over the 5 to 60 μg Chl cm^{-2} range (22). Thus, although the increase in light-harvesting and electron transport components increased light absorption to some extent, it was clearly insufficient to produce the large increase observed in *P*/area.

The idea that *P*/area might be related quantitatively to Chl content was proposed over 50 years ago (6, 9, 25). More recently, Šesták (16) and Buttery and Buzzell (4) have observed relationships between photosynthesis and Chl content. Gabrielson (8), however, disputed the existence of such relationships on the theoretical grounds that Chl content should only influence photosynthesis under low light when *P*/area is directly proportional to light intensity. Hesketh (10) came to a similar conclusion after observing that *P*/area in nine crop species did not appear to be correlated with light absorption or Chl content. However, as Alberte *et al.* (1) point out, *P*/area is more likely to be related to the numbers of reaction centers and electron carriers associated with increased Chl rather than with increased Chl *per se*.

Just how a change in photochemical capacity might influence photosynthesis is not clear. Several mechanisms have been proposed. Farquhar *et al.* (7) suggest that photosynthetic electron transport capacity affects the rate of regeneration of RuBP directly via the rate of supply of ATP and NADPH. Alternatively, inasmuch as several enzymes of the photosynthetic carbon reduction cycle are known to be light activated (3), RuBP regeneration and therefore photosynthetic rate may be regulated by their activity (2). Sicher and Jensen (17) and Perchorowicz *et al.* (14) have suggested that the photochemical reactions (as mediated by changes in irradiance) control the level of activation of RuBPCase. These investigators believe that, since RuBP concentrations in the

chloroplast are high over a wide range of irradiances, the rate of regeneration of RuBP is not limiting photosynthesis.

In conclusion, it seems from these data that the rate of photosynthesis of sugar beets under field conditions may well be co-limited by light-harvesting and electron transport capacity, and that this effect is mediated via photochemical conversion rather than by increased light absorption. In addition, *P*/area is almost certainly colimited by several other internal factors simultaneously, including stomatal and mesophyll conductance, and the kinetic properties of RuBPCase and other enzymes of the Calvin cycle. The photosynthetic apparatus has apparently developed in such a way as to achieve a remarkable balance in the capacities of each part of the total system so that no one part dominates in the control of photosynthetic rate.

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