The significance of differences in the mechanisms of photosynthetic acclimation to light, nitrogen and CO₂ for return on investment in leaves

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Summary
1. We report changes in photosynthetic capacity of leaves developed in varying photon flux density (PFD), nitrogen supply and CO₂ concentration. We determined the relative effect of these environmental factors on photosynthetic capacity per unit leaf volume as well as the volume of tissue per unit leaf area. We calculated resource-use efficiencies from the photosynthetic capacities and measurements of leaf dry mass, carbohydrates and nitrogen content.
2. There were clear differences between the mechanisms of photosynthetic acclimation to PFD, nitrogen supply and CO₂. PFD primarily affected volume of tissue per unit area whereas nitrogen supply primarily affected photosynthetic capacity per unit volume. CO₂ concentration affected both of these parameters and interacted strongly with the PFD and nitrogen treatments.
3. Photosynthetic capacity per unit carbon invested in leaves increased in the low PFD, high nitrogen and low CO₂ treatments. Photosynthetic capacity per unit nitrogen was significantly affected only by nitrogen supply.
4. The responses to low PFD and low nitrogen appear to function to increase the efficiency of utilization of the limiting resource. However, the responses to elevated CO₂ in the high PFD and high nitrogen treatments suggest that high CO₂ can result in a situation where growth is not limited by either carbon or nitrogen supply. Limitation of growth at elevated CO₂ appears to result from internal plant factors that limit utilization of carbohydrates at sinks and/or transport of carbohydrates to sinks.

Key-words: Carbohydrates, A/C response, Glycine max, sink strength, water content

Introduction

The photosynthetic capacities of leaves can change dramatically in response to photon flux density (PFD, Boardman 1977; Björkman 1981), nitrogen supply (Hunt, Weber & Gates 1985) or atmospheric CO₂ concentration (Gunderson & Wullschleger 1994; Griffin & Seemann 1996). All of these responses ultimately must result from changes either in leaf thickness, and thus the quantity of photosynthetic tissue per unit leaf area, or the photosynthetic capacity per unit volume of that tissue. These two modes of response may have quite different implications for resource allocation. Reductions in leaf thickness reduce investment of all resources equally per unit leaf area whereas reductions in photosynthetic enzyme concentrations, which contain a large fraction of total leaf nitrogen (Evans 1989), may reduce nitrogen investment much more than carbon investment.

Changes in photosynthetic capacity in response to light environment result primarily from changes in leaf thickness and thus the quantity of photosynthetic tissue per unit area (Ludlow & Wilson 1971; Louwerse & Zweerde 1977; Patterson, Bunce & Alberte 1977; Patterson, Duke & Hoagland 1978; Sims & Pearcy 1992). This reduces resource investment per unit leaf area of shade leaves and allows greater total leaf area production and thus increased light capture and photosynthesis under light-limiting conditions (Björkman 1981; Givnish 1988; Sims & Pearcy 1994; Sims, Gebauer & Pearcy 1994).

Growth in elevated CO₂ has been reported to increase leaf thickness of soybean (Thomas & Harvey 1983; Leadley et al. 1987; Vu, Allen & Bowes 1989), wheat (Robertson & Leech 1995), sweet gum and pine (Thomas & Harvey 1983), ryegrass (Ferris et al. 1996) and poplar (Radoglou & Jarvis 1990). However, these increases in leaf thickness are generally less than 20%,
much less than the two- to threefold increases reported for acclimation to high PFD. Photosynthetic capacities per unit leaf area of plants grown at elevated CO₂ often decline even though leaf thickness is increased (Gunderson & Wullschleger 1994). Consequently, in contrast to PFD acclimation where photosynthetic capacity per unit investment remains fairly constant (Sims & Peacey 1989), acclimation to elevated CO₂ appears to reduce photosynthetic capacity per unit carbon investment.

Photosynthetic acclimation to elevated CO₂ may instead improve nitrogen-use efficiency. Elevated CO₂ increases the efficiency of Rubisco, the primary carboxylating enzyme of photosynthesis, and thus may allow a decrease in the investment in Rubisco relative to other photosynthetic components (Sage 1990). Because Rubisco accounts for up to 30% of total leaf nitrogen (Evans 1989; Evans & Seemann 1989), reductions in this enzyme could result in substantial savings in nitrogen investment. Nitrogen concentrations of elevated CO₂ grown plants almost always decline (Luo, Field & Mooney 1994) but whether this results in increased photosynthetic nitrogen-use efficiency depends on the relative magnitude of changes in nitrogen content and photosynthetic capacity. It has also been suggested that elevated CO₂ limits nitrogen uptake (Jackson & Reynolds 1996) and thus might result in a response similar to the response to limited nitrogen supply.

Our objective in this study was to determine how the different mechanisms of photosynthetic acclimation to PFD, nitrogen supply and CO₂ affect resource-use efficiency in soybean. We measured the effect of these treatments on photosynthetic capacity per unit tissue volume as well as the change in tissue volume per unit area. Dry mass, non-structural carbohydrates and nitrogen content were used as measures of resource investment. The results are discussed in terms of the possible functions of these responses.

Materials and methods

PLANT MATERIAL AND GROWTH CONDITIONS

Seeds of a non-nodulating 'Lee' variety of soybean, *Glycine max* (Hartwig 1994), were planted in 8 l pots in a 50:50 vol/vol mixture of fine sand and sandy loam topsoil. The pots were placed in naturally lit growth chambers inside a greenhouse at the Desert Research Institute in Reno, NV, USA. Temperatures were controlled to 28±2 °C in the daytime and 20±1 °C at night. Relative humidity at midday was 66±7%.

Two experiments were conducted over consecutive growing seasons. In the first experiment, five growth chambers were used. Each growth chamber was controlled to a different CO₂ concentration (280, 350, 525, 700 or 1000 p.p.m.). Within each chamber there were two levels of PFD (2.32±0.24 or 22.9±2.2 mol m⁻² day⁻¹) and two levels of nitrogen supply (0.75 or 7.5 mM nitrate). In the second experiment four growth chambers were used. Two were controlled to 350 p.p.m. CO₂ and the other two were at 700 p.p.m. CO₂. Within each pair of chambers four PFDs (ranging from 2.25 to 17.9 mol m⁻² day⁻¹) were established. The highest and lowest PFDs were in one chamber and the two intermediate PFDs were in the other chamber. Five nitrogen treatments (0–7.5 mM nitrate) were applied to the plants in the highest PFD treatment while the lower PFD plants received only two different nitrogen treatments (0.75 and 7.5 mM nitrate). There were four plants per treatment except for the five nitrogen levels in the highest PFD where there were only three plants.

CO₂ concentration in each chamber was measured once every 6 min by an infra-red gas analyser (model 6262, LICOR Inc, Lincoln, NE, USA). A datalogger (model CR10, Campbell Scientific, Logan, UT, USA) collected the data and controlled the duration of CO₂ injection into the chambers on a 30 s cycle to maintain the CO₂ setpoint. Because the ambient CO₂ concentration within the greenhouse was quite variable, CO₂ scrubbers were used in the 280 and 350 p.p.m. chambers to maintain a constant CO₂ concentration. The scrubber boxes measured 14 cm x 45 cm x 56 cm high and were constructed from Plexiglas with two fans in the top and an open grill covered by screening in the bottom. In the first experiment, CO₂ in the air flowing through the boxes was absorbed by cooler pads ('Coolpad' brand, Research Products Corp., Avondale, AZ, USA) dipped in a slurry of hydrated lime (Chemical Lime Co., Scottsdale, AZ, USA) and water. In the second experiment, CO₂ was absorbed by soda lime ('Sodaorb' brand, W.R. Grace & Co., Atlanta, GA, USA). These boxes were placed inside the chambers and the fans were operated continuously. Control to the setpoints was achieved through additions of CO₂.

Each chamber was divided into high and low PFD halves. The front (south) half received full sun or slightly reduced PFD under neutral density black plastic shade cloth (40% grade). The back (north) half received lower PFDs under thicker shade cloth (60 and 90%). PFD was measured continuously throughout the experiments with one gallium arsenide photodiode (model G1118 Hamamatsu Corp., Bridgewater, NJ, USA) in each PFD treatment connected to a data-logger (model CR10, Campbell Scientific, Logan, UT, USA). These sensors were previously calibrated against a quantum sensor (model 190 s, LI-COR Inc., Lincoln, NE, USA). The mean daily PFD over the 4–6 week growing period of the plants was used in the data analysis.

Nutrient treatments were randomly arranged within the light and CO₂ treatments. Nutrient treatments were begun 3 days following seedling emergence. All plants received either a half-strength Hoagland solution (7.5 mM NO₃, 0.5 mM PO₄, 3 mM K, 2.5 mM Ca, 1 mM Mg, 1 mM SO₄, 0.067 mM Fe-EDTA, plus
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GAS-EXCHANGE MEASUREMENTS

Photosynthesis of one leaf per plant was measured after 4–6 weeks growth. Measurements were made on fully expanded leaves two nodes down from the youngest expanding leaf greater than 1 cm long. This leaf was found to have the highest photosynthetic rates in preliminary measurements of all leaves on three high- and three low-CO2 grown plants (data not shown). Because we wanted to compare plants at similar developmental stages, measurements were made on the higher PFD plants before the lower PFD plants, which grew more slowly.

Photosynthesis was measured in an open flow gas-exchange system (model 6400, LICOR Inc., Lincoln, NE, USA). CO2 and O2 concentrations in the air supplied to the system were controlled by mixing pure O2 and N2 with CO2 in N2 using mass flow controllers (model 825, Edwards High Vacuum International, Wilmington, MA, USA). An O2 concentration of 21% was used for all measurements. Dew-point of the air was controlled by a dew-point humidifier (model DPH02, Armstrong Enterprises, Palo Alto, CA, USA). The light source for all measurements was a tungsten halogen projector lamp (model ENH, 120 V-250 W, Radiac Inc, Japan) reflected off a 45° cold mirror.

The response of assimilation to intercellular CO2 concentration was measured at PFDs exceeding light saturation for the leaf. Measurement PFDs for high photosynthetic capacity sun grown leaves were 1200–1400 μmol m⁻² s⁻¹ but this was reduced to around 800 μmol m⁻² s⁻¹ for shade leaves to avoid problems with photo-inhibition. Leaf temperature was 28 °C and water-vapour concentration was 30±2 mmol mol⁻¹. Leaves were initially allowed to equilibrate for 30 min at 350 p.p.m. CO2, then the CO2 concentration was reduced to =80 p.p.m. and subsequently increased in eight steps to =1000 p.p.m. allowing 6–10 min for equilibration at each CO2 concentration. The measured responses of assimilation to intercellular CO2 concentration (A/Ci curves) were fit to a photosynthesis model (Farquhar, von Caemmerer & Berry 1980) for estimation of carboxylation capacity (Vcmax).

LEAF CHARACTERISTICS

Leaf samples were collected from the same leaves used in the gas-exchange measurements. Prior to collection of the leaves, the plants were returned to the growth chambers for 1 day and then leaves were collected in the mid-afternoon. Collection at a consistent time of day reduced variation owing to diurnal changes in carbohydrate contents. In preliminary experiments we found diurnal fluctuations of 10% or more in leaf dry mass per unit area but less than 2% changes in leaf water content. Central leaflets were detached from the plant and the midrib excised. One half of the leaflet was weighed as quickly as possible (less than 1 min) after detachment from the plant to determine fresh mass. Leaf area was then measured with an area meter (model 3000, LI-COR Inc., Lincoln, NE, USA) and the samples were dried for 48 h at 60 °C prior to determination of dry mass and total nitrogen content (model 2400 CHN analyser, Perkin Elmer, Norwalk, CT, USA). The other half of the leaflet was frozen in liquid nitrogen and stored in a −80 °C freezer until they were analysed for glucose, fructose, sucrose and starch using the technique of Hendrix (1993).

Results

The effect of growth CO2 on photosynthesis (measured at light saturation and the growth CO2 concentration) depended on the PFD and nitrogen treatments (Fig. 1 and Table 1; note the significant three-way interaction in Table 1). Photosynthesis of high PFD/high-nitrogen plants increased strongly with CO2 up to 700 p.p.m. and then declined at 1000 p.p.m. In contrast, photosynthesis of the high PFD/low-nitrogen plants changed very little across the growth CO2 gradient. For low PFD plants, photosynthesis increased with CO2 in both high and low nitrogen treatments.

Photosynthesis at the growth CO2 was a function of both direct effects of CO2 on photosynthetic rates and indirect effects of light, nitrogen and CO2 on photo-

![Fig. 1. Photosynthesis measured at the growth CO2 concentration and light saturation (Agrow) for plants grown in a range of CO2 concentrations and PFDs of 18 mol (photon) m⁻² day⁻¹ (open symbols) or 2-3 mol (photon) m⁻² day⁻¹ (filled symbols) and nitrogen supplies of 7.5 mm nitrate (circles) or 0.9 mm nitrate (triangles).](image-url)
Table 1. Significance levels for the effect of light, nitrogen and CO₂ treatments on photosynthesis measured at light saturation and the growth CO₂ concentration (A$_{grow}$), carboxylation capacity [V$_{\text{cmax}}$, calculated from the response of assimilation to intercellular CO₂ concentration and expressed per unit leaf area (area), leaf nitrogen (N), leaf dry mass (DM) or leaf water content (w)], leaf dry mass per unit area (h), TNF free leaf dry mass per unit area (h$_s$), nitrogen as a percentage of leaf dry mass (n$_m$), nitrogen as a percentage of TNF free leaf dry mass (n$_s$), nitrogen per unit leaf area (n$_a$), leaf water content per unit area (w, leaf fresh mass minus dry mass), and total non-structural carbohydrates as percentage of leaf dry mass (TNC). Individual carbohydrates; glucose (glu), fructose (fru), sucrose (suc) and starch (st), each expressed per unit leaf area (area) or per unit leaf water content (w) were only measured in the second experiment. Interaction terms for which there were no significant effects are not listed. Significance levels: *** P < 0.001; ** P < 0.01; * P < 0.05.

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Changes in leaf non-structural carbohydrate content (TNC) can dramatically affect leaf dry mass without having any effect on actual leaf thickness and volume. Expressing V$_{\text{cmax}}$ per unit leaf water content (V$_{\text{cmax}}$/w) eliminates the effect of TNCs and provides a measure of the average concentration of photosynthetic components in the cell solution. On this basis, PFD had very little effect on V$_{\text{cmax}}$ (Fig. 2j). At 350 p.p.m. CO₂, V$_{\text{cmax}}$/w increased strongly with increasing nitrogen supply up to 4 mM nitrate and then declined (Fig. 2k). At 700 p.p.m. CO₂, V$_{\text{cmax}}$/w was relatively constant except for a drop at the lowest nitrogen supply. Consequently, the CO₂ effect on V$_{\text{cmax}}$/w was much greater at intermediate nitrogen supplies. This appears to account for the lack of a significant CO₂ effect on dry mass (V$_{\text{cmax}}$/DM), a measure of the return on carbon investment, which was increased at the lowest PFDs but otherwise was little affected by PFD (Fig. 2g).
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Fig. 2. Carboxylation capacity ($V_{\text{max}}$, estimated from the response of assimilation to intercellular CO2 concentration) expressed per unit leaf area, per unit leaf nitrogen (N), per unit leaf dry mass (DM) or per unit leaf water content for plants grown in a range of photon flux densities (PFD), nitrogen supplies and CO2 concentrations. Symbols for PFD gradient: 700 p.p.m. CO2 (open symbols), 350 p.p.m. CO2 (filled symbols), 7.5 mM nitrate (circles) and 0.9 mM nitrate (triangles). Symbols for nitrogen gradient: 700 p.p.m. CO2 (open symbols) and 350 p.p.m. CO2 (filled symbols). Symbols for CO2 gradient: 18 mol (photon) m$^{-2}$ day$^{-1}$ (open symbols) and 2.3 mol (photon) m$^{-2}$ day$^{-1}$ (filled symbols), 7.5 mM nitrate (circles) and 0.9 mM nitrate (triangles). Arrows indicate resource levels used in the other gradients.

$V_{\text{max}}/w$ in the CO2 gradient experiment (Fig. 2l) where only the high and low nitrogen treatments were used.

Leaf dry mass per unit area (LMA) is the sum of non-structural carbohydrates (TNC) and TNC free dry mass, where the latter should be related to the structural investment in the leaf. Increasing PFD increased LMA (Fig. 3a) as a result of increases in both TNC (Fig. 3d) and TNC free dry mass (Fig. 3g). The increase in TNC was particularly large from the lowest to the second lowest PFD for the high CO2 plants (Fig. 3d). Increasing nitrogen supply decreased TNCs (Fig. 3e) but increased TNC free dry mass (Fig. 3h) resulting in no change in LMA (Fig. 3b). Elevated CO2 resulted in increased TNC (Fig. 3f) and thus LMA (Fig. 3c) but had little effect on TNC free dry mass (Fig. 3i). The CO2 effects were much greater at high than at low PFD. Responses of leaf water content...
per unit area ($w$, an estimate of leaf thickness, Fig. 3j–l) were qualitatively similar to responses of TNC free leaf dry mass (Fig. 3g–i) except for a greater CO$_2$ effect on $w$ at intermediate nitrogen supply (Fig. 3k).

Starch accounted for more than 90% of the TNC content (Fig. 4) and consequently the responses of starch content to PFD, nitrogen and CO$_2$ were similar to those observed for TNC. The responses of soluble carbohydrates were quite different from those of starch. When expressed per unit area, glucose increased with increasing PFD (Table 1, Fig. 4a) and was higher at elevated CO$_2$ concentration (Fig. 4a,b). There was an interaction between nitrogen supply and CO$_2$ concentration such that the soluble carbohydrate contents were greatest at high CO$_2$ and intermediate nitrogen (Fig. 4b,d,f). For fructose and sucrose there was an interaction between PFD and CO$_2$ such that the CO$_2$ effect was greater at higher PFD (Table 1, Fig. 4c,e).

The PFD effect on soluble sugar contents was largely a result of increased leaf thickness. PFD had no significant effect on glucose and fructose concentration expressed per unit leaf water (i.e. average

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Fig. 3. Leaf dry mass per unit area, total non-structural carbohydrates (TNC) as a percentage of leaf dry mass, TNC free leaf dry mass per unit area and leaf water content (fresh mass minus dry mass) per unit area for plants grown in a range of photon flux densities (PFD), nitrogen supplies and CO$_2$ concentrations. Symbols are as in Fig. 2.
Similarly, increasing nitrogen supply resulted in a large increase in $n_a$ at high PFD (Fig. 5b) but had little effect at low PFD (Fig. 5a). At low PFD, CO$_2$ had little effect on $n_a$ (Fig. 5c) but, at high PFD, $n_a$ decreased slightly with increasing CO$_2$ concentration.

Increasing PFD had little effect on leaf nitrogen as percentage of dry mass regardless of whether it was expressed per unit total dry mass (Fig. 5d) or LNC free dry mass (Fig. 5g), suggesting that the increase in $n_a$ with high PFD resulted primarily from increases in LMA. In contrast, increasing nitrogen supply resulted in proportional increases in $n_a$ (Fig. 5b) and $n_m$ (Fig. 5e) suggesting that the increase in $n_a$ resulted entirely from increases in $n_m$ rather than LMA.

Elevated CO$_2$ concentration decreased nitrogen concentration across all treatments when nitrogen concentration was expressed per unit total dry mass (Fig. Sd-f). Expressing percentage nitrogen on a TNC free dry mass basis eliminated the CO$_2$ effect in many but not all cases (Fig. Sg–i).

Discussion

There were clear differences between the mechanisms of photosynthetic acclimation to PFD, nitrogen supply and CO$_2$. Acclimation to PFD resulted largely from changes in leaf thickness and thus the quantity of photosynthetic tissue per unit area rather than changes in photosynthetic capacity per unit volume of tissue. In contrast, limited nitrogen supply had little effect on leaf thickness but substantially reduced photosynthetic capacity per unit volume of tissue. Elevated CO$_2$ concentration also decreased photosynthetic capacity per unit tissue volume and this effect was most pronounced at intermediate nitrogen supply. This interaction between nitrogen supply and CO$_2$ highlights the complexity of CO$_2$ responses and the need for multi-factor experiments. The CO$_2$ responses in the PFD and CO$_2$ gradients might have been substantially greater had an intermediate nitrogen supply been used in addition to the high and low nitrogen treatments. Elevated CO$_2$ increased leaf thickness but this effect was much smaller than the effect on leaf dry mass per unit area. The greater effect on leaf dry mass was the result of increased total non-structural carbohydrate content (TNC) in the elevated CO$_2$ leaves.

These different mechanisms of acclimation have important consequences for the return on investment in leaves. Acclimation to high PFD decreased photosynthetic capacity per unit dry mass but had little effect on photosynthetic capacity per unit nitrogen. Low nitrogen supply increased photosynthetic capacity per unit nitrogen but decreased photosynthetic capacity per unit dry mass. Elevated CO$_2$ decreased photosynthetic capacity on both dry mass and nitrogen bases.

The differences in return on investment provide insight into whether these responses could function to increase acquisition of a limiting resource.
Conversely, they also suggest when growth is not limited by resource supply. The increase in photosynthetic capacity per unit dry mass of shade leaves is consistent with a carbohydrate limitation of growth in low PFD. Conversely, the reduction in photosynthetic capacity per unit dry mass as PFD increases suggests that the increase in photosynthetic capacity per unit area of sun leaves does not directly function to increase carbon gain. Whole plant carbon gain as a percentage of dry mass (which is proportional to relative growth rate), for shade acclimated plants measured at PFDs sufficient to saturate photosynthesis, has been found to be equal to or greater than that of sun acclimated plants (Blackman & Wilson 1954; Hughes 1966; Rice & Bazzaz 1989; Sims & Pearcy 1994; Sims, Gebauer & Pearcy 1994). This is possible because the reduced photosynthetic capacity per unit leaf area of shade plants is compensated for by increased total leaf area. Instead of directly increasing carbon gain, sun-leaf characteristics may function to reduce the susceptibility of leaves to damage under stressful conditions. Sun leaves are less susceptible to photoinhibition (Björkman 1981) but this may be function of increases in xanthophyll cycle pigment contents (Demmig-Adams et al. 1995; Koniger et al. 1995) as well as increases in photosynthetic capacity.

Whereas PFD primarily affected photosynthetic capacity per unit dry mass, changes in nitrogen supply affected the return on investment for both carbon and nitrogen. At low nitrogen supply, photosynthetic capacity per unit nitrogen is increased while photosynthetic capacity per unit dry mass is decreased. As nitrogen supply increases, photosynthetic capacity per unit nitrogen decreases but photosynthetic capacity per unit dry mass increases, suggesting a shift from nitrogen to carbon limitation of growth.

If elevated CO₂ resulted in increased nitrogen limitation as has been proposed (Jackson & Reynolds 1996), we would expect a shift to greater nitrogen-use efficiency with increasing CO₂. However, we found no significant effect of elevated CO₂ on photosynthetic capacity per unit nitrogen. Also, elevated CO₂ resulted in increased w whereas limiting nitrogen
Acclimation to light, N and CO₂ generally decreased w, suggesting that these are in fact distinct responses. These results, combined with the large accumulation of non-structural carbohydrates in elevated CO₂ leaves, suggest that growth under elevated CO₂ is not limited by either carbon or nitrogen supply.

Even in the absence of a nitrogen limitation elevated CO₂ increases the efficiency of Rubisco and thus might allow reductions in the investment in Rubisco relative to other photosynthetic components (Sage 1990). Because Rubisco accounts for up to 30% of total leaf nitrogen (Evans 1989; Evans & Seemann 1989) this could have a substantial effect on nitrogen investment. However, our results suggest that any increase in nitrogen-use efficiency is quite small and thus is probably not the primary factor driving response to elevated CO₂.

An emphasis on resource-use efficiency makes the assumption that growth is primarily resource limited. This is no doubt the case in low-PFD and low-nitrogen environments but may not be true for elevated CO₂ combined with high PFD and high nitrogen. Instead of improving resource-use efficiency, photosynthetic acclimation to elevated CO₂ may be a response to limited plasticity in sink demand for carbon (Stitt 1991) and/or limited ability to move carbohydrates from the sites of photosynthesis to the sink tissues. The large increases in leaf TNC content of elevated CO₂ grown plants suggest such a limitation. We have already argued that growth of elevated CO₂ plants does not appear to be nitrogen limited. Sink strength might be limited by other factors such as temperature (Hofstra & Hesketh 1975) or maximal rates of cell division and expansion (Kinsman et al. 1996). However, some studies suggest that the limitation involves export of carbon and transport to sinks rather than limited sink demand. In a study of carbohydrate production and utilization in soybean, Cure, Rufty & Israel (1991) concluded that rates of phloem loading and/or sucrose synthesis, rather than sink demand, limited carbohydrate export from source leaves. A similar conclusion can be drawn from studies currently underway in our laboratory. Treatment of single soybean leaflets with high CO₂, while the rest of the plant remained at ambient CO₂, resulted in carbohydrate accumulation in the treated leaflet to levels similar to those of leaflets where the whole plant was exposed to high CO₂ (D. A. Sims, unpublished data).

Carbohydrate accumulation in leaves is often correlated with reduced photosynthetic capacity of elevated CO₂ grown plants (Stitt 1991). This might result from interactions between carbohydrates and hexokinase leading to changes in the rate of synthesis of several photosynthetic enzymes (Jang & Sheen 1994). However, we found no overall correlation between whole leaf sugar concentrations, or the change in these sugar concentrations with growth in elevated CO₂, and changes in Vₘₐₓ per unit volume. Also, in the experiments mentioned above, treatment of single leaflets with elevated CO₂ substantially increased sugar concentrations but had no effect on photosynthetic capacity. Further evidence that photosynthetic responses are not a simple function of sugar concentrations comes from studies of plants transformed to express the movement protein from tobacco mosaic virus. These plants accumulate carbohydrates in their leaves without significant effects on photosynthesis (Lucas et al. 1996).

These results suggest that photosynthetic responses at the leaf level may be a function of the integrated control of growth and development throughout the plant. An understanding of these responses will require an understanding of both the limitations to growth and resource utilization, and the signals which act to maintain a balance between resource uptake and utilization. This may require an understanding of internal limitations to carbohydrate utilization, such as limitations on the rate of transport to sinks in addition to the effects of external environmental conditions. Future efforts to predict photosynthetic acclimation to CO₂ should focus on the factors limiting growth under natural conditions as well as the signals linking a growth limitation at sinks to photosynthetic responses of sources.

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References


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