Impact of measurement irradiance on acclimation of photosynthesis to elevated CO_2 concentration in several plant species

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Abstract

Controlled environment chamber and glasshouse studies were conducted on six herbaceous annual species grown at 350 (AC) and 700 (EC) $\mu mol(CO_2)$ mol^{-1} to determine whether growth at EC resulted in acclimation of the apparent quantum yield of photosynthesis (QY) measured at limiting photosynthetic photon flux density (PPFD), or in acclimation of net photosynthetic rate (P_N) measured at saturating PPFD. It was also determined whether acclimation in P_N at limiting PPFD was correlated with acclimation of carboxylation efficiency or ribulose-1,5-bisphosphate (RuBP) regeneration rate measured at saturating PPFD. Growth at EC reduced both the QY and P_N at limiting PPFD in three of the six species. The occurrence of photosynthetic acclimation measured at a rate limiting PPFD was independent of whether photosynthetic acclimation was apparent at saturating measurement PPFD. At saturating measurement PPFD, acclimation to EC in the apparent carboxylation efficiency and RuBP regeneration capacity also occurred independently. Thus at least three components of the photosynthetic system may adjust independently when leaves are grown at EC. Estimates of photosynthetic acclimation at both high and low PPFD are necessary to accurately predict photosynthesis at the whole plant or canopy level as [CO_2] increases.

Additional key words: acclimation; CO_2-enrichment; photon flux density; quantum yield.

Introduction

Most of the reports concerning acclimation of photosynthesis to increasing atmospheric CO_2 concentration (cf. the review of Saralabai *et al.* 1997) have dealt only with photosynthetic rates of single leaves measured at a high photosynthetic photon flux density (PPFD). This is true even in studies where acclimation was examined as a function of position within a canopy (*e.g.*, Kubiske *et al.* 1997, Osborne *et al.* 1998, Sims *et al.* 1999). There are relatively few studies which have

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determined whether acclimation of photosynthesis occurs at measurement PPFDs that limits photosynthesis. Models predicting photosynthesis at EC assume that no acclimation will occur in PPFD-limited P_N even if it occurs for PPFD-saturated photosynthesis, and that PPFD-limited P_N will be stimulated by EC in a temperature dependent manner (Long 1991, Kirschbaum 1994). Because P_N is often limited by low PPFD, the occurrence of acclimation of quantum yield (QY) to growth at EC would have important implications for predicting the response of whole plant or canopy photosynthesis to increasing atmospheric [CO_2].

Long and Drake (1991) showed conclusively that no acclimation of the QY at limiting PPFD occurred in *Scirpus olneyi* after several years of growth at about twice the current concentration of carbon dioxide. However, at that time there was also no apparent acclimation of P_N measured at high PPFD in that species (Ziska *et al.* 1990). Acclimation of photosynthesis at high PPFD sometimes occurs without acclimation in QY at limiting PPFDs (*e.g.,* Ziska *et al.* 1991, Osborne *et al.* 1997). The few reports suggesting that acclimation of P_N to EC measured at low PPFD may occur (Grulke *et al.* 1993, Sicher *et al.* 1995, 1997) also found acclimation at high measurement PPFD. Because it has not often been assessed, it is unclear how common acclimation of P_N at limiting PPFD may be and whether it can occur without acclimation being evident at high PPFD. The purpose of this work was to determine whether acclimation in the apparent QY of photosynthesis occurred in response to EC for a range of species, and whether acclimation in QY, carboxylation efficiency, and RuBP regeneration capacity were correlated within a species.

Materials and methods

One set of experiments was conducted using *Glycine max* L. cv. Clark grown in controlled environment chambers under artificial light. Chamber air temperature was 25±0.2 °C, and radiant energy from a mixture of metal halide and high pressure sodium lamps at a PPFD of 900 μmol m^{-2} s^{-1} was provided for 14 h per day. The concentration of CO_2 was controlled at either 350 or 700 ± 20 μmol mol^{-1} by injecting CO_2 or CO_2-free air under the control of an infrared analyzer which sampled chamber air continuously. Plants were grown one per 4 000 cm^3 pot filled with vermiculite and watered daily with a complete nutrient solution containing 13.5 mM nitrogen (Robinson 1984). Measurements of photosynthetic properties were made on third trifoliolate leaves within a few days after full expansion. Leaf absorbance of the radiant energy used in the gas exchange measurements was determined from incident, transmitted, and reflected PPFD measured with a quantum sensor for individual leaves grown at AC and EC. The two growth [CO_2] conditions were established in three independent replicates. No differences among replicates occurred, and a growth [CO_2] effect was tested using the values combined across replicates.

Plants for all other experiments were grown in sunlit glasshouses in order to provide the plants with natural variation in PPFD. Two identical air conditioned glasshouses were used. CO_2 was injected into the glasshouses to maintain

concentrations of either AC or EC, as controlled by absolute infrared CO$_2$ analyzers which sampled the air continuously. The day/night temperatures were 28/19 °C, each ±2 °C. Daytime air temperatures were maintained for 12 h per day beginning 4 h before solar noon. Blowers circulated air continuously and produced an air speed of about 0.5 m s^{-1} over the plants. The glasshouses transmitted approximately 65 % of the incident PPFD on a daily basis, although peak PPFDs were within 10 % of those AC concentrations and shaded, ventilated air temperatures were sampled every 5 s and means recorded every 15 min. Long-term mean air temperatures in the two glasshouses were indistinguishable. Plants were grown one per pot in plastic pots filled with vermiculite and flushed daily with the nutrient solution. The size of the pots used varied depending on the species and the duration of the experiment, but did not restrict growth, as determined by comparison with plants in smaller pots.

Four experiments were conducted in the glasshouses between the months of March and October in 1996, 1997, and 1998. CO$_2$ treatments were switched between glasshouses between experiments. The values were analyzed assuming that [CO$_2$] was the sole treatment variable between the glasshouses. In one experiment, *Hordeum vulgare* L. cv. Brant, *Lycopersicon esculentum* Mil. cv. Rutgers, *Solanum melongena* L. cv. Black Beauty, and *Vicia faba* L. cv. Long Pod were grown for about 4 weeks and leaf photosynthetic gas exchange characterized for the most recently fully expanded leaves. A similar study was conducted on six cultivars of *G. max* (Avery, Flyer, Regal, Ripley, Spencer, and Stafford), and photosynthetic properties of third trifoliolate leaves characterized within a few days after full area expansion. In another experiment with *G. max* cultivars Avery, Clark, D70-6545, Fiskeby, L62-1579, and Spencer, photosynthetic properties of second trifoliolate leaves were measured at 20-22 d after planting, when they were recently fully expanded, and again at 38-40 d after they had been shaded by higher leaves. In another experiment, plants of *Chenopodium album* L. were grown for 33 d in the glasshouses, and photosynthetic properties characterized.

Leaf photosynthetic CO$_2$ exchange properties were characterized using either of two gas exchange analysis systems, a *CIRAS-1* portable photosynthesis system with a broad-leaf chamber and halogen lamp (*PP Systems*, Haverhill, MA, USA), or a laboratory made open system described in Wilson and Bunce (1997). All measurements were made at the daytime growth temperature, and with a water vapor pressure deficit of less than 1.5 kPa. The portable system was used in the glasshouse experiments with the four species, and in the glasshouse experiments examining third trifoliolate leaves in *G. max*. For the experiment examining the age effects in *G. max* and the experiments on *C. album*, plants were moved into a controlled environment chamber for measurement with the laboratory made system. Parallel measurements were made using both gas exchange systems for the *G. max* plants grown in the controlled environment chamber. For all experiments, P_N was determined at AC and EC at a minimum, and usually for a wider range of [CO$_2$] allowing assessment of the apparent carboxylation efficiency from the initial slope, and the rate of RuBP regeneration from the rate at EC, using the method of Wullschleger (1993). These measurements of P_N responses to [CO$_2$] were made at both a PPFD of >1500 μmol m^{-2} s^{-1}, which was found to be saturating, and also at a rate-limiting PPFD of 400

μmol m^{-2} s^{-1} or less. In experiments with *G. max* in the controlled-environment chamber, and in the experiments with the four species, QY was determined from the slope of the response of P_N to incident PPFD in the range of 90 to 150 μmol m^{-2} s^{-1}. These PPFD were chosen since we determined them to be above those where QY was influenced by the Kok effect. QY was measured before exposing plants to the high PPFD used in determining the CO_2-response at high PPFD. This was done in order to avoid possible photoinhibition by the high PPFD used for the CO_2-response measurements.

Results

In *G. max* grown in controlled-environment chambers, QY was lower in leaves developed at EC when measured at AC or EC (Table 1). In these leaves, P_N at high PPFD was also lower (Table 1). Similar results were obtained with both gas exchange measurement systems (not shown). Leaves from both CO_2 treatments absorbed 0.85±0.02 of the incident PPFD.

Table 1. Apparent quantum yields, QY [mol mol^{-1}] of photosynthetic carbon dioxide assimilation of third trifoliolate leaves of *G. max* cv. Clark grown in a controlled environment chamber at external [CO_2] of 350 (AC) or 700 (EC) μmol mol^{-1}. Both types of measurement were done at either AC or EC, the QY at PPFDs of 90 to 150 μmol m^{-2} s^{-1}, and net photosynthetic rates (P_N) [μmol m^{-2} s^{-1}] at PPFD of 1600 μmol m^{-2} s^{-1} and air temperature of 25 °C. Means are ±SE for $n = 10$. Growth and measurement [CO_2] effects were both significant at $p = 0.05$ for QY and P_N.

Growth [CO_2]	Measurement [CO_2]			
	AC	EC	AC	EC
	QY		P_N	
AC	0.048±0.001	0.060±0.001	31.0±0.5	50.4±2.2
EC	0.037±0.003	0.049±0.003	20.2±0.9	41.0±1.4

When third trifoliolate leaves of six cultivars of *G. max* were examined at full area expansion for plants grown in the glasshouse at AC and EC, acclimation of P_N to EC was not evident at high measurement PPFD, but acclimation of P_N measured at low PPFD was sufficient to eliminate photosynthetic stimulation by EC (Table 2). A similar result was obtained with *C. album*, with no evidence of photosynthetic acclimation at EC for measurements made at high PPFD, but acclimation was evident when measured at a lower PPFD (Fig. 1*A,B*). Acclimation at low measurement PPFD eliminated any net stimulation of P_N by EC at the growth [CO_2] at low PPFD for both species.

In the experiment examining the effect of age on photosynthetic responses of second trifoliolate leaves of *G. max* grown in the glasshouse, no acclimation of P_N occurred at any measurement PPFD at 20-22 d after planting (Fig. 1*C,D*). However, older leaves exhibited acclimation of photosynthesis sufficient to eliminate the stimulation by growth at EC at all measurement PPFDs (Fig. 1*C,D*).

Table 2. Net photosynthetic rates (P_N) [μmol m^{-2} s^{-1}] measured at 150 (P_{N150}) or 1600 (P_{N1600}) μmol m^{-2} s^{-1} PPFD at [CO_2] of 350 (AC) or 700 (EC) μmol mol^{-1} for third trifoliolate leaves of six cultivars of *Glycine max* (Avery, Flyer, Regal, Ripley, Spencer, and Stafford) grown in the glasshouse at AC or EC. Measurements were made at an air temperature of 28 °C. There were no significant diffferences among cultivars, and values are means ± SE for n = 30. Growth and measurement [CO_2] effects were both significant at p = 0.05 for quantum yield and P_N.

Growth [CO_2]	Measurement [CO_2]	P_{N150}	P_{N1600}
EC	AC	4.30±0.09	28.50±0.62
EC	EC	6.20±0.07	31.80±0.46
AC	AC	6.20±0.12	54.00±0.73
AC	EC	9.39±0.10	56.20±0.87

In the experiment with four species grown in the glasshouse, QY was reduced by growth at EC in *V. faba*, but not in the other species (Table 3). In *V. faba*, the CO_2-saturated P_N was also reduced by growth at EC, but the initial slope was unaffected (Table 3). In *H. vulgare*, EC increased both carboxylation efficiency and RuBP regeneration capacity, whereas both were reduced in *S. melongena*. In *L. esculentum*, EC reduced carboxylation efficiency but not RuBP regeneration capacity (Table 3).
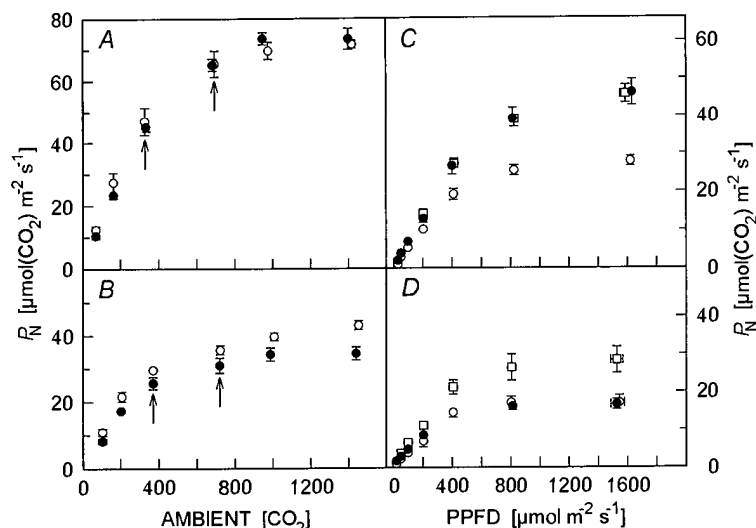

Fig. 1. Responses to the [CO_2] external to the leaf of net photosynthetic rate (P_N) measured at high (1750-1765 μmol m^{-2} s^{-1}) (*A*) or low (402-415 μmol m^{-2} s^{-1}) (*B*) photosynthetic photon flux (PPFD), or responses of P_N to PPFD in 20-22 d (*C*) or 38-40 d (*D*) old leaves of *Chenopodium album* plants grown at 350 (AC, *open symbols*) or 700 (EC, *filled symbols*) μmol(CO_2) mol^{-1}. *Arrows* in *A* and *B* indicate the growth [CO_2]. Each point represents a mean of 3 leaves. *C* and *D* show means of 3 leaves of each of six cultivars, Avery, Clark, D70-6545, Fiskeby, L62-1579, and Spencer, measured at the growth [CO_2]; plants grown at AC were also measured at EC (▫). Vertical bars represent SE of the mean.

Table 3. Apparent quantum yield (QY) [μmol mol^{-1}] of CO_2 assimilation at [CO_2] = 350 μmol mol^{-1} at limiting PPFDs, initial slope of P_N/C_i [mol m^{-2} s^{-1}] at a PPFD of 1500 μmol m^{-2} s^{-1}, and the CO_2 saturated net photosynthetic rate (P_N) [μmol m^{-2} s^{-1}] at a PPFD of 1500 μmol m^{-2} s^{-1}, measured at an air temperature of 28 °C, for four plant species grown in a glasshouse at 350 (AC) or 700 (EC) μmol(CO_2) mol^{-1}. Means ± SE are given for n = 4 or 5; * indicates a significant effect of growth [CO_2] at p = 0.05.

Species	Growth [CO_2]	QY	Initial slope	Saturated P_N
Hordeum vulgare	AC	41.5±2.0	0.179±0.017*	39.9±1.0*
	EC	42.0±4.0	0.234±0.009	44.4±1.3
Lycopersicon esculentum	AC	43.7±1.0	0.161±0.003*	31.2±1.4
	EC	44.3±1.0	0.132±0.006	32.2±1.5
Solanum melonghena	AC	45.7±1.0	0.190±0.004*	34.2±0.6*
	EC	46.0±1.0	0.170±0.006	31.5±1.1
Vicia faba	AC	55.8±3.0*	0.195±0.003	45.3±1.0*
	EC	47.0±2.0	0.196±0.011	41.0±1.2

Discussion

Our present results indicate that acclimation to EC can, in some species, reduce the QY of photosynthetic CO_2 assimilation and reduce P_N measured at limiting PPFDs. Either reduced QY or reduced P_N at limiting PPFDs were found in three of the six species examined in this study, in *C. album*, *G. max*, and *V. faba*. In this study, acclimation in P_N measured at limiting PPFD in some cases occurred when there was no evidence of photosynthetic acclimation at high measurement PPFD, while in other cases acclimation was also evident at high measurement PPFD. This independence of acclimation measured at low and high PPFD agrees with the lack of correlation among species in the amount of photosynthetic acclimation to EC measured at high and limiting PPFDs (Bunce 1997). Differences between photosynthetic acclimation to EC measured at high and low PPFD may also partly explain the discrepancy between the temperature dependence of the stimulation of P_N by EC when comparing single leaves with whole plants (Ziska and Bunce 1997). Mechanisms of reduction in QY at EC were not investigated here, but reductions in QY in response to several stresses, such as water stress, chilling, and photoinhibition occur, and can be caused by damage to the photosystems or by patchy stomatal closure.

In four of the six species, apparent carboxylation efficiency (initial slope) and RuBP regeneration capacity (CO_2-saturated rate) were independent in their response to growth at EC. Similar independence of acclimation in apparent carboxylation efficiency and RuBP regeneration capacity were reported by Sage *et al.* (1989). For plants grown at AC, apparent carboxylation efficiency and RuBP regeneration capacity are tightly correlated in species comparisons (Wullschleger 1993, Leuning 1997). Apparently growth at EC can disrupt this correlation.

Two recent hypotheses have been advanced as explanations for photosynthetic acclimation to EC. A reduction in apparent carboxylation efficiency relative to RuBP regeneration capacity at EC may represent a beneficial reallocation of nitrogen from ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) into processes which become more rate limiting to photosynthesis at EC (*e.g.,* Ziska *et al.* 1991, Sage *et al.* 1997). Secondly, the small subunit of RuBPCO and a few other nuclearly coded photosynthetic genes are sometimes selectively repressed by excessive saccharides at EC (*e.g.,* Sheen 1994, Van Oosten *et al.* 1994). Whether RuBP regeneration capacity is significantly controlled by the enzymes repressed by excessive saccharides is not yet clear, but RuBPCO activity is often reduced (*e.g.,* Osborne *et al.* 1997, Sage *et al.* 1997, Van Oosten *et al.* 1994, Sharma-Natu *et al.* 1997). These two hypotheses imply either selective repression of carboxylation efficiency or coordinated repression of both carboxylation efficiency and RuBP regeneration capacity by growth at EC. There seems to be more diversity in the types of acclimation of photosynthetic processes to EC than would be implied by these two hypotheses. At present, several seemingly independent acclimation responses may occur at EC, a reduction in QY, increases or decreases in apparent carboxylation efficiency, and increases or decreases in RuBP regeneration capacity. There are as yet insufficient results to identify patterns about the occurrence of these various responses.

Whether all our results would extrapolate to outdoor conditions is unknown. There are now sufficient results to indicate that acclimation of photosynthesis measured at high PPFD can occur under field conditions in response to growth at EC (*e.g.,* Bunce 1995, Sicher *et al.* 1995, Osborne *et al.* 1997, Bryant *et al.* 1998, Roberntz and Stockfors 1998). However, acclimation of QY of photosynthesis has seldom been examined under field conditions. No acclimation in QY was found in *Scirpus olneyi* after several years of exposure to EC (Long and Drake 1991). In another study, the evidence was somewhat ambiguous: while mean values of QY were reduced by as much as 20 % by growth at EC in *Duchesnea indica*, this reduction was not significant with three replicates (Osborne *et al.* 1997). In spring wheat, plants grown at EC did not have higher rates of assimilation in late afternoon on most measurement days, despite higher midday P_N (Garcia *et al.* 1998). Although not discussed by the authors, this pattern would be consistent with a larger P_N at limiting than at saturating PPFD. In sunlit chambers tracking ambient temperature and humidity conditions, EC increased QY on only 2 of 5 measurement days in Douglas fir seedlings (Lewis *et al.* 1999), suggesting that acclimation of QY to growth at EC occurred.

Because changes in QY, carboxylation efficiency, and RuBP regeneration capacity affect P_N under different environmental conditions, such as high and low PPFD, high and low temperature, and high and low CO$_2$ availability, the seemingly independent acclimation of these to EC greatly complicates predictions of photosynthetic responses to the ongoing increase in AC. Because most assays of photosynthetic acclimation to EC have routinely been made at high PPFD, it may be especially important that in some cases acclimation was sufficient to eliminate any increase in P_N at the growth [CO$_2$] when measurements were made at limiting PPFD, even when there was no evidence of photosynthetic acclimation for measurements at high PPFD.

Recognition that three photosynthetic parameters, QY, carboxylation efficiency, and RuBP regeneration capacity, may have different responses to [CO_2] during development may eventually improve the ability to scale plant responses to rising AC from the single leaf level to that of whole plants or canopies and across environments.

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