Regular paper

The effect of free air carbon dioxide enrichment (FACE) and soil nitrogen availability on the photosynthetic capacity of wheat

F. Miglietta[1], A. Giuntoli[1] & M. Bindi[2]
[1]*IATA-CNR Institute of Agrometeorology and Environmental Analysis, National Research Council of Italy, P. le delle Cascine 18, 50144 Florence, Italy;* [2]*CeSIA – Accademia dei Georgofili, Logge Uffizi Corti, 50122 Florence, Italy*

Abstract

A simple system for free air carbon dioxide enrichment (FACE) was recently developed and it is here briefly described. Such a MiniFACE system allowed the elevation of CO_2 concentration of small field plots avoiding the occurrence of large spatial and temporal fluctuations. A CO_2 enrichment field experiment was conducted in Italy in the season 1993–1994 with wheat (cv. Super-dwarf Mercia). A randomized experimental design was used with the treatment combination $CO_2 \times$ soil N, replicated twice. Gas exchange measurements showed that photosynthetic capacity was significantly decreased in plants exposed to elevated CO_2 and grown under nitrogen deficiency. Photosynthetic acclimation was, in this case, due to the occurrence of reduced rates of rubP saturated and rubP regeneration limited photosynthesis. Gas exchange measurements did not instead reveal any significant effect of elevated CO_2 on the photosynthetic capacity of leaves of plants well fertilized with nitrogen, in spite of a transitory negative effect on rubP regeneration limited photosynthesis that was detected to occur in the central part of a day with high irradiance. It is concluded that the levels of nitrogen fertilization will play a substantial role in modulating CO_2 fertilization effects on growth and yields of wheat crops under the scenario of future climate change.

Abbreviations: A:C_i – assimilation (A) *versus* intercellular CO_2 concentration (C_i); Ca – CO_2 concentration surrounding the leaf; FACE – Free Air CO_2 Enrichment; IRGA – infrared gas analyser; Jmax – light saturated rate of electron transport; P_i – inorganic phosphorus; rubP – Ribulose-1,5-bisphosphate; Vcmax – maximum rubP rate of carboxylation

Introduction

A number of experiments have already demonstrated that carbon uptake rates, biomass accumulation and yield are increased when C_3 agricultural species, including wheat, are exposed to enhanced atmospheric CO_2 concentrations (Kimball 1983; Wittwer 1984; Lawlor and Mitchell 1992; Idso and Idso 1994). This CO_2-fertilization effect is a direct consequence of the fact that increased atmospheric CO_2 inhibits oxygenation of Ribulose-1,5-bisphosphate (rubP) thus partially suppressing photorespiration (Jordan and Ogren 1984) and increases the velocity of carboxylation reaction leading to increased substrate binding (Stitt 1991).

Acclimatory downward regulation of photosynthetic capacity has been often, but not always, observed in C_3 plants after long term exposure to elevated CO_2 (Sage et al. 1989; Long and Drake 1992), and it is now accepted that photosynthetic acclimation under conditions of elevated CO_2 is not only an artifact due to growing conditions (Arp 1991; Stitt 1991; Sage 1994). Several potential mechanisms leading to acclimation under conditions of elevated CO_2 have been extensively reviewed (Stitt 1991; Woodrow 1994), but the excessive accumulation of carbohydrates in leaves is

accepted to be one of the most important determinants of acclimation (Stitt 1991; Sage 1994; Webber et al. 1994). Such accumulation can lead to feed-back inhibition of photosynthesis through an increase in phosphorylated intermediates sequestering part of the cytosolic P_i and leading to an inhibition of ATP synthesis (Sharkey 1985), through adjustments of the concentrations of photosynthetic enzymes (Stitt 1991) or the repression of photosynthetic gene expression (Webber et al. 1994; Sheen 1994; van Oosten et al. 1994).

Whatever the case, increased carbon uptake which is initially promoted by increased CO_2 concentration alters the balance between the supply and the capacity to use carbohydrates so that plants may be unable to use the excess carbon fixed under elevated CO_2 (Körner and Miglietta 1994). Accordingly, feed-back inhibition of photosynthesis under elevated CO_2 is most likely in plants that are least able to generate new sinks for carbon and use additional carbohydrates in respiration, growth and storage (Gifford 1992; Long and Drake 1992). Such limitations are expected to occur in nitrogen limited plants as these are unable to generate new sinks for carbohydrates in response to increased photosynthate supply (Spiertz et al. 1977; Vos 1981; Triboi and Ollier 1991) and, hence, to remobilize, during night, temporary storage carbohydrate pools that accumulated during the day (Fichtner et al. 1993; Schnyder 1993; Paul and Stitt 1993; Webber et al. 1994).

There are a few studies on the combined effects of elevated CO_2 concentration and nitrogen shortage on the occurrence of photosynthetic acclimation in wheat (Petterson and Mc Donald 1994). Full season experiments made with this species in the laboratory gave contradictory results. Mitchell et al. (1993) found no evidence for acclimation of photosynthesis at two levels of CO_2 and two levels of N application; in another experiment photosynthetic capacity was significantly reduced under elevated CO_2 only in nitrogen deficient plants (S.P. Long, pers. comm.), and, in a third laboratory study, significant downward regulation of photosynthetic capacity was found under full nutrient supply (McKee and Woodward 1994). It is uncertain if results obtained in laboratory experiments can be directly extrapolated to plants grown under field conditions. Free air CO_2 enrichment (FACE) experiments can potentially reduce those uncertainties (Hendrey and Kimball 1994), and, accordingly, a simple fumigation facility (MiniFACE) was developed to grow plants under otherwise natural field conditions in the open. In this paper, performances of the fumigation device are

at first illustrated and, then, leaf gas exchange results are reported and discussed.

Materials and methods

The MiniFACE facility

Free air CO_2 enrichment (FACE) has been successfully achieved in a series of innovative experiments made over the last five years on cotton (Hendrey and Kimball 1994) and wheat (Pinter et al. 1993) in the US. These experiments made use of sophisticated FACE technologies developed by the Brookhaven National Laboratory of the Department of Energy of the United States (Lewin et al. 1992). The MiniFACE facility used in this experiment is a much simpler system that makes use the same concepts adopted by FACE technology on a smaller scale. Briefly, the fumigation device consists of an horizontal pipe connected to a square plenum (both of 8 cm diameter) which rests on the soil surface and encloses an area of 1 m^2 (Figure 1). Air is blown into the plenum by a fan (OMIE, Florence) with a capacity of a 10 m^3 min^{-1} and is vented upward from a number of small holes of 0.5 cm diameter. CO_2 is added to the air stream by injecting pure carbon dioxide 30 cm after the blower. Turbulent mixing of the air venting out of the plenum and of atmospheric air affects the CO_2 concentration of the atmosphere surrounding plants growing in the MiniFACE plot. Given a constant CO_2 injection rate, the higher the windspeed, the faster the mixing and the lower the CO_2 concentration measured downwind of the plenum. This principle has been used to develop a computer-controlled system to keep the CO_2 concentration constant above the area of MiniFACE plots. This system allows to control CO_2 injection rates into the air stream by means of a computer-controlled mass flow controller (0–30 L min^{-1}, Unit Instruments, Ireland). Injection rates are at first calculated from wind velocity measured by a cup anemometer located near the MiniFACE setup and, then, these are corrected using a feedback control algorithm. The PID (Proportional Integral Differential) algorithm used for MiniFACE is the same described by Lewin et al. (1992) and makes use of windspeed and CO_2 concentration measurements made by an infrared gas analyzer (PPS EGM-1, Hitchin) in the center of the plot. The gas analyzer has a measuring range of 0–2000 μmol mol^{-1}, an accuracy of 1% full scale and a time resolution of 1 s. The IRGA used in the MiniFACE is designed to smooth fluctuations in CO_2
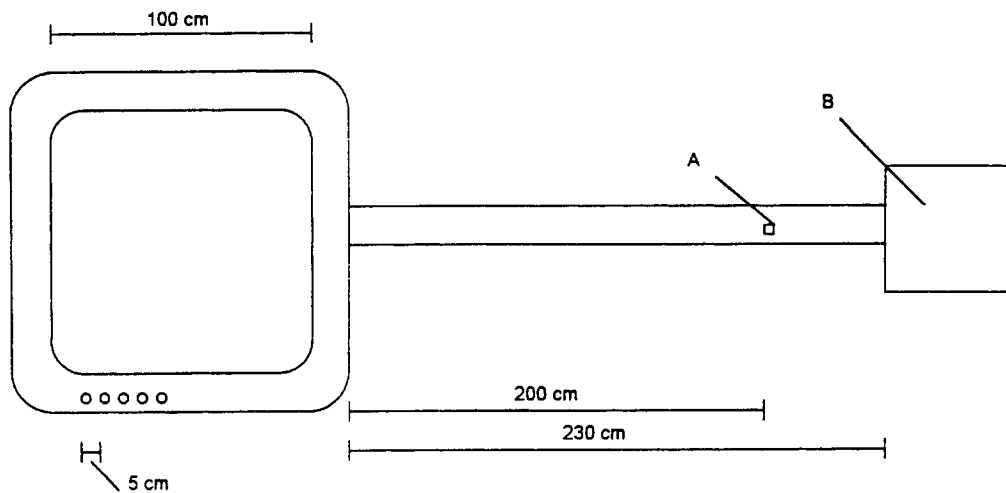
Figure 1. Sketch diagram of the MiniFACE plot showing dimensions and spatial arrangements of components: A = CO$_2$ injection point, B = fan.

concentration; when the difference between two consecutive readings is smaller than the 1% of the first reading, the output value is calculated as the mean of the two readings rather than just the value of the second reading. If the difference between the two readings exceeds this 1% threshold, the exact value of the second reading is given as output. Such smoothing function has practically no consequences on the long term mean of CO$_2$ concentration and very little effect on variability as the probability to have a difference smaller than 1% in the MiniFACE system is extremely low (data not shown). Wind velocity and CO$_2$ injection rates are respectively read and calculated every second. The whole MiniFACE setup is operated by a single IRGA and air sampling is alternatively made at the center of each CO$_2$ enriched plot using a multiport sampler. Air is sampled by a 50 L min^{-1} pump and the length of sample lines (6 mm diameter tubes) is 10 m. This allows the air sample to traverse this length in less than 7 s. Frequency of CO$_2$ transfer between plots is 15 minutes.

Tests made on a MiniFACE prototype design showed that system performances were little affected by the height of the vegetation when this remained below 50 cm. Accordingly, taller vegetation is unsuitable for this specific design. Short term measurements made during prototype development showed that there were minimal interferences between adjacent enriched and control plots when the distance between them is greater than 2.5 m. However, such an interference effect was not measured in detail during the experiment as CO$_2$ concentration in the center of the control
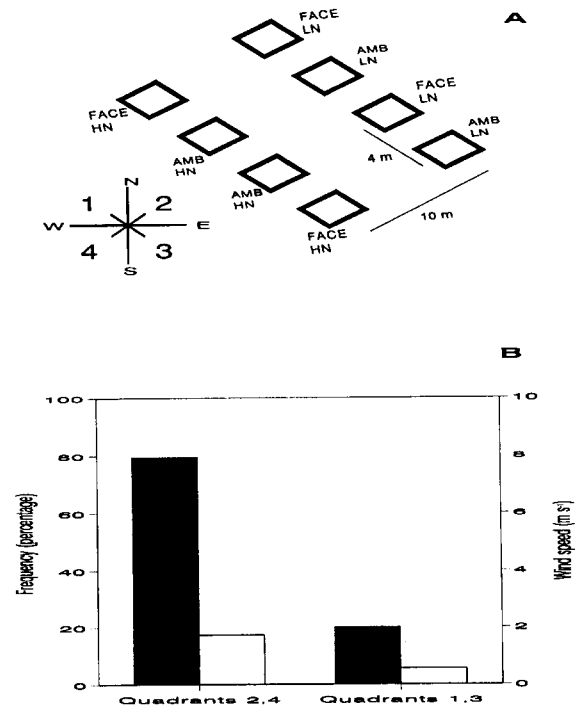

Figure 2. (A) Spatial layout of MiniFACE plots used for the experiment (HN = high nitrogen, LN = low nitrogen, FACE = elevated CO$_2$, AMB = ambient CO$_2$). Geographical orientation is given in the figure; quadrants are numbered clockwise. (B) Frequency of wind directions and wind speed from the four quadrants measured during the experiment. Data are grouped into two classes showing that prevailing wind direction could have caused only minimal interferences between enriched and control plots. Wind speed empty bars, wind direction filled bars.

plots was not measured. Nevertheless, it is obvious that any interference between plots may only have significance for controls when the wind is towards them. Spatial layout of plots in this MiniFACE experiment was such to avoid this effect as the plots were oriented to take into account the prevailing wind direction (Figure 2).

System performances were evaluated in the season 1993–1994 by continuously recording in computer files 1 minute average values of wind velocity, CO_2 injection rates and CO_2 concentrations measured in the center of the plots. Spatial distribution of CO_2 concentrations within MiniFACE rings were also monitored both for 40 minutes with an IRGA and for 6 hours using Draeger diffusion tubes during the growing season. IRGA measurements were made in a windy day using an automatic multiport sampler (ACME Instruments, Florence); eight sampling tubes (6 mm diameter) were placed at canopy height 10 cm apart along a transect traced along wind direction and air pumped from each sampling point to an IRGA at a rate 50 L min^{-1}. CO_2 concentrations were monitored for 5 consecutive minutes at each sampling point and 1 minute averages of IRGA readings made every second were stored in a computer file. Other measurements were made using diffusion tubes (Draeger, Lübeck, Germany). These tubes provide an estimate of average CO_2 concentrations by the visual estimation of colour changes of a specific reactant along a graded scale. Thirty nine tubes were evenly spaced over the MiniFACE plot and readings were made after 6 hours. One tube was placed at a distance of a few millimetres from the IRGA probe in the center to allow a comparison of average CO_2 concentration measured by the IRGA and by the diffusion tubes.

Experimental design, physiological measurements and data analysis

A MiniFACE experiment was made in the season 1993–1994 in Rapolano Terme, Siena, where the availability of large quantities of pure geologic CO_2 provided an inexpensive source of gas for experiments (Miglietta et al. 1993). A super-dwarf winter wheat variety (cv. Super-dwarf Mercia) was chosen for the experiment as its maximum height was well below the maximum value above which MiniFACE performances could be reduced. An experimental design was used with the treatment combination CO_2 × soil N, replicated twice. In order to avoid gradients in soil conditions over the experimental field, experimental

plots were at first excavated and the original soil was replaced by an homogeneous sandy clay loam substrate containing 0.07% of total N, 9.6 μmol mol^{-1} of P and 99.5 μmol mol^{-1} of K. Plot size was 4 m^2 and the MiniFACE systems were placed in the center of each plot to avoid edge effects. There were no restrictions in the lateral area or depth that roots of plants growing within the MiniFACE plots could exploit. The distance between fumigated plots was higher than 2.5 meters and this distance proved to be sufficient to avoid any interference between plots.

Plants were sown on 27 November 1993 in rows 11 cm apart and plant density at emergence was 250 plants m^{-2}. All the plots were well watered throughout the growing season and were abundantly fertilized with K (15 g m^{-2}) and P (8 g m^{-2}). Nitrogen was added to fertilized plots in the form of urea 3 times during the growing season (sowing, tillering and terminal spikelet stages) for a total amount of 15.6 g m^{-2}. The plots were harvested on 14 July 1994. CO_2 fumigation, that was made both during the day and at night, started at the time of sowing and was interrupted on 8 July 1994 when grains were considered to have reached full physiological maturity. Target CO_2 concentration was kept constant at 600 μmol mol^{-1} throughout the whole growing season. There were only three interruptions of fumigation during the experiment due to equipment maintenance and power supply failure, and the longest interruption lasted 36 hours.

Assimilation *versus* intercellular CO_2 concentration (A:C_i) was measured by gas exchange using an open portable photosynthesis system (CIRAS-1, PPS, Hitchin) between 15 May and 15 June 1994. The last fully expanded leaf was enclosed in an artificially illuminated, temperature controlled and ventilated cuvette and measurements were made at leaf temperatures comprised between 23 and 28 °C. Measurements were made in the early morning, in the late afternoon, after dusk and on overcast days both to reduce risks of uncontrolled heating of the leaf chamber and the occurrence of disturbing variable effects of diurnal changes in leaf photosynthetic capacity. Leaf water vapour pressure deficit was kept almost constant (1 KPa) during measurements by controlling both the temperature and the humidity of air entering the cuvette. A:C_i response was measured by changing the CO_2 concentration of air entering the cuvette (Ca) into 7 steps (100, 200, 350, 700, 1000, 1500, 2000 μmol mol^{-1}) and recording gas exchange parameters when all variables were steady. In addition to A:C_i curves, a set of gas exchange measurements was taken on 17 May 1994 on 20 leaves in
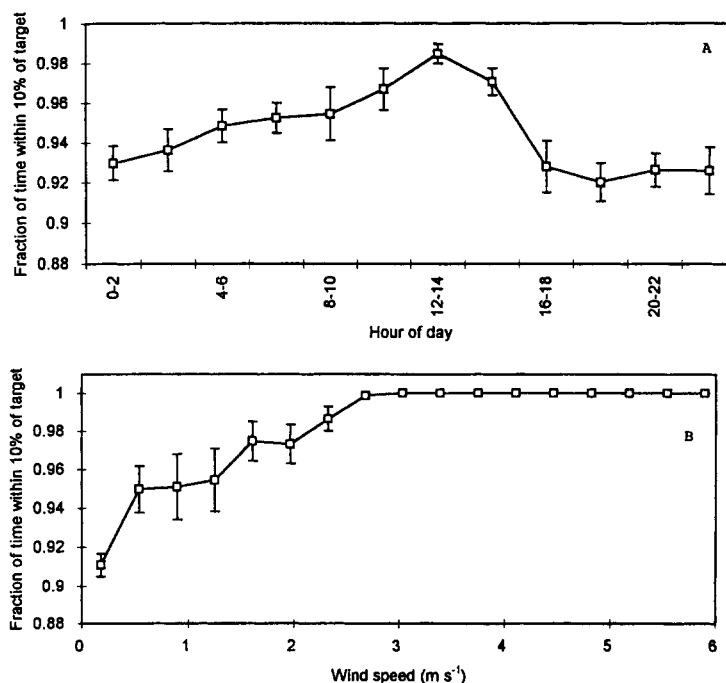
Figure 3. MiniFACE performances: effect of hour of day (A) and of wind velocity (B). Data shown is the fraction of time in which 1 minute average CO_2 concentrations measured at the center of the MiniFACE plot were within 10% of target (y-axis). Frequencies were calculated over the entire fumigation period.

each nitrogen fertilized plot using constant Ca values of 1500 μmol mol^{-1}. Also in this case measurements were taken with all the variables steady.

The biochemical model developed by Farquhar et al. (1980) and Farquhar and von Caemmerer (1982) was fitted to each measured $A{:}C_i$ curve by iteratively adjusting the values of the maximum rubP rate of carboxylation (Vcmax) and the light saturated rate of electron transport (Jmax) until the mean square error calculated between observations and model estimates was minimized. The procedure used for model fitting was similar to that used by Harley et al. (1992). Incorporation of triose phosphate limitation of photosynthesis into the model (Harley et al. 1992) did not improve substantially model fitting. Model parameters were those of the original model as modified by Long (1991). Temperature dependence of the different biochemical parameters was considered while fitting the model; values of Vcmax and Jmax at 25 °C were used for statistical analysis using multifactorial analysis of variance.

Table 1. Seasonal mean and standard deviation of 1 minute average CO_2 concentration for the four plots

	Plot 1	Plot 2	Plot 3	Plot 4
Mean	604.12	606.81	607.81	604.91
Standard deviation	43.04	43.06	42.55	37.50

Results and discussion

MiniFACE performances

Mean long-term CO_2 concentrations measured over the entire fumigation period in the center of CO_2 enriched MiniFACE plots were very close to target concentration. There were no appreciable differences in the mean CO_2 concentration and standard deviation between the fumigated plots (Table 1). Provided this small variability among the plots, subsequent performance data are shown as combined plot data. CO_2 control was better during the day than at night (Figure 3a) and better under windy than under calm conditions (Figure 3b). CO_2 concentrations measured in the center of the
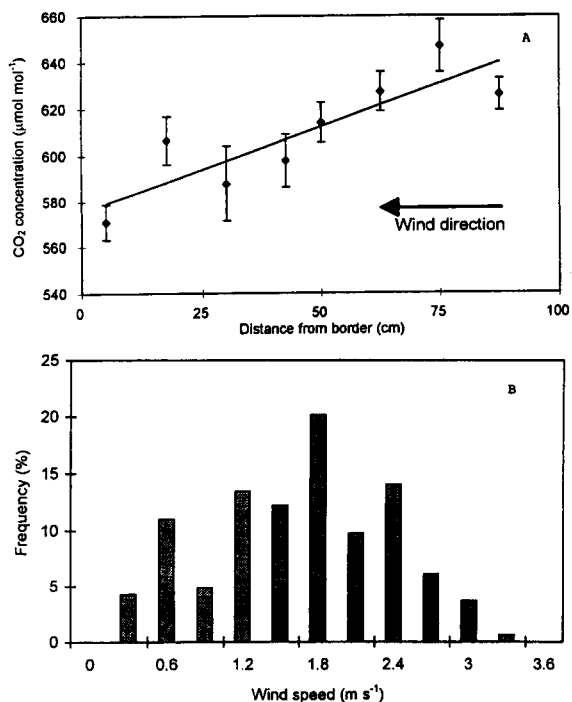
Figure 4. Short-term measurements of CO_2 concentration gradient measured along wind direction in the MiniFACE plot (A). Vertical bars are standard errors of 1 minute average of IRGA readings taken over a period of 40 minutes (see text for explanation). Wind direction is indicated by the horizontal arrow. Frequency distribution of 1 minute average wind speed during the measurement period is shown on plate (B).

Figure 5. Contour plot of CO_2 concentrations measured by means of Draeger diffusion tubes over six hours. The square area delimited by the solid line indicates the surface of the MiniFACE plot. Gradient analysis was made by regression of CO_2 concentrations measured along the 4 axes shown in the figure. Regression coefficients (r) were 0.16, 0.14, 0.04, 0.08 for AB, CD, EF and GH directions, respectively. None of the regressions was significant for $P \leq 0.05$.

fumigated plots were within 10% of the target concentration (600 μmol mol^{-1}) for more than 90% of the time (Figure 3). Under windy conditions, CO_2 concentrations measured with the IRGA along a transect traced along wind direction were higher upwind than downwind, but the difference between the two opposite MiniFACE sides was smaller than 60 μmol mol^{-1} (Figure 4). Wind speed during measurements is also shown in the Figure 4.

CO_2 concentration measurements made over six hours with diffusion tubes clearly showed the lack of any significant gradient of CO_2 concentration over the entire MiniFACE area (Figure 5). Both IRGA and Draeger tubes measurements were made over a very limited time. This implies that the whole range of atmospheric stabilities and wind velocity conditions were unlikely to be fully represented.

Canopy development did not affect MiniFACE performances as CO_2 concentrations measured in the center of the plots before and after stem elongation were comparable (data not shown).
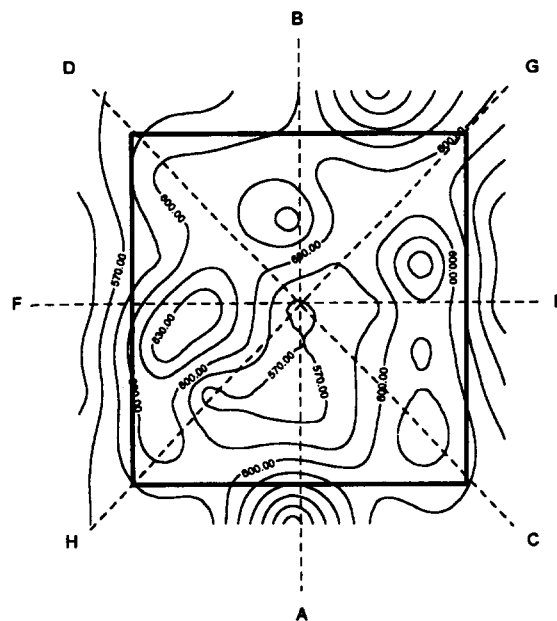
Photosynthetic capacity under low nitrogen

The Farquhar and von Caemmerer biochemical model of photosynthesis fitted accurately to the A:C_i response curves measured by gas exchange (Table 2). At variance analysis, both atmospheric CO_2 concentration and nitrogen fertilization had significant effects on the calculated photosynthetic parameters (Jmax and Vcmax). The $CO_2 \times N$ interaction was also significant (Table 2). Both Jmax and Vcmax were lower at ambient CO_2 concentration and low N than at ambient CO_2 and high N. Although this difference was significant only at P=0.10 (Table 2), it reflected the occurrence of reduced photosynthetic capacity in plants grown under severe nitrogen deficiency.

Elevated atmospheric CO_2 concentration had a significant negative effect on both rubP saturated (Vcmax) and rubP limited (Jmax) rates of carbon fixation of plants grown under nitrogen deficiency (Table 2 and Figure 6). This type of acclimatory response involving inhibition of assimilation rate at all C_i levels was already observed in CO_2 enrichment experiments (Sage 1994) and implies proportional changes in all components of the photosynthetic apparatus. It has

Table 2. Mean values (± mean standard error) and analysis of variance of Jmax and Vcmax calculated by fitting the Farquhar and van Caemmerer model to the A:C$_i$ curves measured in the MiniFACE plots. Values of the Root Mean Square Error (RMSE) and number of measured curves (*n*) are reported in the table. Different letters following the mean values indicate significant differences at 5% level using LSD multiple range test

	Jmax	Vcmax	RMSE	*n*
Low nitrogen/elevated CO$_2$	157.9 ± 15.9a	54.4 ± 12.7a	2.01	10
Low nitrogen/ambient	241.8 ± 16.7b	116.9 ± 12.6b	1.75	9
High nitrogen/elevatedCO$_2$	266.2 ± 15.6b	119.4 ± 11.9b	1.96	10
High nitrogen/ambient	281.8 ± 17.8b	128.6 ± 14.3b	1.64	7
Main effects				
Nitrogen	$P = 0.0001$	$P = 0.0056$		
CO$_2$	$p = 0.0052$	$P = 0.0092$		
Interaction				
CO$_2$ × nitrogen	$P = 0.0468$	$P = 0.0470$		

Table 3. Mean assimilation (A), stomatal conductance (g$_s$) and intercellular CO$_2$ concentration (C$_i$) measured on fertilized MiniFACE plots (ambient and elevated CO$_2$) in the central part of the day on 17 May 1994 using a constant C$_a$ of 1500 μmol mol^{-1}. Observed assimilation rates are compared with values calculated by the model fitted to the A:C$_i$ curves (Model)

	Model	A	G$_s$	C$_i$
Elevated CO$_2$	43.5	34.9 ± 0.62	192.6 ± 8.9	1087.3 ± 87.4
Ambient	46.4	43.7 ± 0.41	432.0 ± 41.2	1181.7 ± 93.6

been postulated that partial suppression of photorespiration in elevated CO$_2$, could favour transfer of nitrogen investments from Rubisco to the light harvesting complex (Long 1991) so that rubP saturated photosynthetic capacity would be decreased and rubP regeneration limited capacity enhanced by elevated CO$_2$ (Long et al. 1993; Sage 1994). Our results did not support this hypothesis for wheat, but instead, the view that Rubisco activity and electron transport capacity were closely coupled (Evans 1989; Stitt and Schulze 1994). Other studies made under low nitrogen availability and elevated CO$_2$ gave similar results (Thomas et al. 1994).

A:C$_i$ curves made on nitrogen deficient wheat leaves indicated that elevated CO$_2$ led to almost complete photosynthetic acclimation as assimilation measured at Ca equal to the growth CO$_2$ concentration was only slightly different between plants grown at ambient and elevated CO$_2$ (Figure 6). Although this observation could not be directly scaled up to the whole canopy, it suggested that the amount of photosynthates made available to the crop by the leaves of the upper canopy layer were not increased in plants grown under elevated CO$_2$.

Photosynthetic capacity under high nitrogen

Photosynthetic capacity of plants grown under abundant nitrogen supply was not affected by elevated CO$_2$ concentration as the small decreases in Jmax and Vcmax were not significant at the variance analysis (Table 2). Accordingly, the CO$_2$-stimulation of leaf photosynthesis in upper canopy leaves was persistent over the entire period of measurements. When calculated by the fitted model, leaf photosynthesis was increased by more than 50% by elevated CO$_2$. The lack of photosynthetic acclimation under elevated CO$_2$ was already observed in other studies made both under controlled conditions (Mitchell et al. 1993; Delgado et al. 1994), and in the field (Garcia et al. 1995). In another study, Mc Kee and Woodward (1994) observed symptoms of P$_i$ limitations (O$_2$ insensitive photosynthesis) in the flag leaf of wheat grown under elevated CO$_2$ and abundant nitrogen supply, but in their experiment pot size used likely restricted rooting volume. Hence, our study confirmed the general view that P$_i$ limitations in elevated CO$_2$ are unlikely when nutrition and rooting volume are not restricted (Sage 1994).

$$A \ (umol \ m^{-2}s^{-1})$$

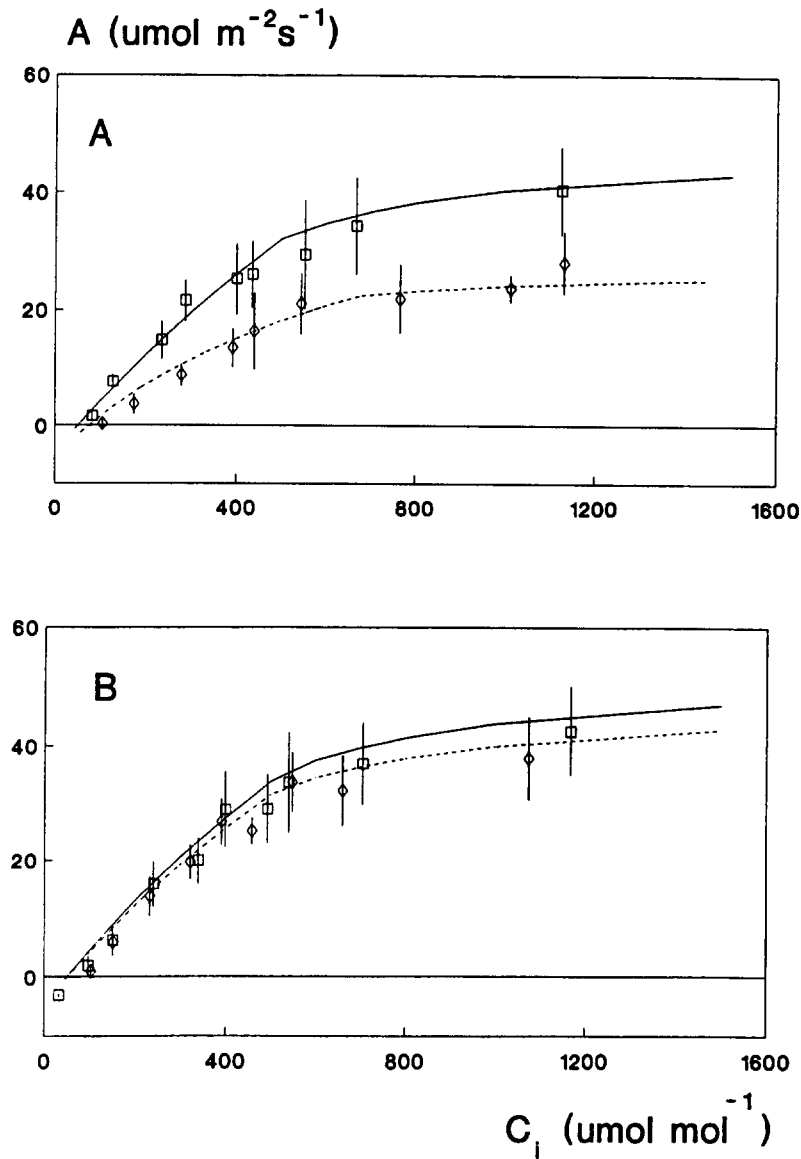$$C_i \ (umol \ mol^{-1})$$

Figure 6. $A:C_i$ curves fitted using the model of Farquhar and von Caemmerer for the different treatments in the MiniFACE experiment. Legend: A = low nitrogen, B = high nitrogen; $\square$, and solid line: ambient; $\Diamond$, and dotted line: elevated CO_2.

Measurements of rubP regeneration limited photosynthetic capacity that were made under conditions of full irradiance at midday on 17 May, showed that for the same C_a of 1500 μmol mol^{-1}, leaves of plants exposed to elevated CO_2 had both lower assimilation rates and lower stomatal conductance than plants grown at ambient CO_2 (Table 3). This difference in conductance prevented a direct comparison of photosynthetic rates of the two groups of plants at the same C_i. However, for the given observed C_i, assimilation rates of leaves exposed to elevated CO_2 were lower

than those predicted by the model fitted to the measured $A:C_i$ curves, whereas this did not happen for plants grown at ambient CO_2 (Table 3). Although such an observation was insufficient for a rigorous statistical analysis, it suggested that a transitory partial inhibition of photosynthesis could have occurred in plants exposed to elevated CO_2 in the central part of clear days. This is well in agreement with a similar observation made in a FACE experiment made with wheat in Arizona, in which the decline in mid-afternoon leaf photosynthesis was larger in plants exposed to elevated

CO_2 than in controls (Garcia et al. 1995). In that study, this transitory inhibition of photosynthesis under elevated CO_2 was associated to a large accumulation of carbohydrates in leaves and, consequently, it was interpreted as the result of P_i sequestration or decreased activation of Rubisco. The capacity for an efficient translocation and remobilization of diurnal temporary storage carbohydrate pool to the large available sinks in plants well supplied with nutrients (Schnyder 1993) can fully explain the transitory nature of such an acclimatory effect and its rapid recovery under conditions of low irradiance.

Conclusions

This work suggested that:

- permanent acclimation of photosynthesis does occur after long-term exposure to elevated CO_2 in field grown wheat when nitrogen is severely limiting;

- this downward regulation is due to both reduced rubP saturated and rubP regeneration limited photosynthetic capacity;

- permanent acclimation does not occur in plants well supplied with nitrogen when these are exposed to elevated CO_2;

- short-term reductions in the rubP regeneration limited photosynthetic rate may occur in leaves of well fertilized plants in the central part of days with high irradiance as likely response to increased carbohydrate accumulation.

The use of the MiniFACE fumigation facility provided an opportunity to obtain these results under realistic field conditions that greatly enhanced their predictive value. These results suggested, for instance, that the levels of nitrogen fertilization will become even more important in determining growth and yield potentials of wheat under the scenario of climate change. Positive CO_2-fertilization effects may be in fact fully offset by reduced carbon fixation capacity under nitrogen shortage, whereas increasing atmospheric CO_2 may significantly enhance carbon uptake and yield in well fertilized crops. Consequences of this biological response on yields achievable in the different agroecological areas of the world can be substantial.

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