Influence of irradiance on photosynthesis and PSII photochemical efficiency in maize during short-term exposure at high CO_2 concentration

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Abstract

This work aimed to evaluate if gas exchange and PSII photochemical activity in maize are affected by different irradiance levels during short-term exposure to elevated CO_2. For this purpose gas exchange and chlorophyll *a* fluorescence were measured on maize plants grown at ambient CO_2 concentration (control CO_2) and exposed for 4 h to short-term treatments at 800 μmol(CO_2) mol^{-1} (high CO_2) at a photosynthetic photon flux density (PPFD) of either 1,000 μmol m^{-2} s^{-1} (control light) or 1,900 μmol m^{-2} s^{-1} (high light). At control light, high-CO_2 leaves showed a significant decrease of net photosynthetic rate (P_N) and a rise in the ratio of intercellular to ambient CO_2 concentration (C_i/C_a) and water-use efficiency (WUE) compared to control CO_2 leaves. No difference between CO_2 concentrations for PSII effective photochemistry (Φ_{PSII}), photochemical quenching (q_p) and nonphotochemical quenching (NPQ) was detected. Under high light, high-CO_2 leaves did not differ in P_N, C_i/C_a, Φ_{PSII} and NPQ, but showed an increase of WUE. These results suggest that at control light photosynthetic apparatus is negatively affected by high CO_2 concentration in terms of carbon gain by limitations in photosynthetic dark reaction rather than in photochemistry. At high light, the elevated CO_2 concentration did not promote an increase of photosynthesis and photochemistry but only an improvement of water balance due to increased WUE.

Additional key words: climate change; elevated CO_2; light intensity; photosynthesis; *Zea mays* L.

Introduction

The rise in the atmospheric CO_2 concentration and the related increase in temperature and changes in precipitation will determine significant effects on terrestrial plant growth and productivity in the next future (Reddy *et al.* 2010). Most of the research about the response to elevated CO_2 has been carried out with C_3 species, where photosynthetic activity was stimulated because of Rubisco carboxylation kinetic properties. The lower attention to C_4 plants in this subject has been attributed to the assumption that the intrinsic CO_2 concentrating mechanism in C_4 plants makes these plants insensitive to atmospheric elevated CO_2 (Reddy *et al.* 2010). However several reports suggest that C_4 photosynthesis also responds to high CO_2. The response of C_4 plants to predicted climate change will play a critical role, as they contribute between 25 and 30% of global primary productivity (Defries and Townsend 1994). Among C_4 plants, *Zea mays* L. is globally one of the most important food crops in terms of production (Young and Long 2000, Leakey *et al.* 2004).

It has been demonstrated that the saturation of C_4 photosynthesis to CO_2 is modified by temperature, irradiance, nutrient availability, and water supply (Loreto *et al.* 1995, Cousins and Bloom 2003, Leakey *et al.* 2006).

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Abbreviations: C_a – ambient CO_2 concentration; C_i – intercellular CO_2 concentration; C_i/C_a – ratio of intercellular to ambient CO_2 concentration; F – the steady-state fluorescence level in the light-adapted status; F_m – the maximal fluorescence level in the dark-adapted state; F_m' – maximal fluorescence level in the light-adapted state; F_0 – the background fluorescence signal; F_0' – the minimal fluorescence yield in light-adapted samples; F_v/F_m – maximum photochemical efficiency of PSII; g_s – stomatal conductance to water; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; q_p – photochemical quenching; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; WUE – water-use efficiency; Φ_{PSII} – the effective quantum yield of PSII photochemistry.

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Some C_4 plants exhibited increased photosynthetic rates in response to CO_2 rising, particularly at elevated temperature and under limiting water supply (Cousin *et al.* 2002, Sage and Kubien 2003, Leakey *et al.* 2009). Ghannoum *et al.* (2000) reported that C_4 plants grown under high irradiance showed enhanced photosynthesis under elevated CO_2 conditions, whereas there was not much response in the growth of C_4 species under low irradiance.

The major mechanisms responsible for the increase of C_4 plant growth under elevated CO_2 seem to be two ones (Ghannoum *et al.* 2000). The first mechanism operates through CO_2-induced increase in net photosynthetic rates. Although it has often been thought that C_4 species are enzymatically saturated with carbon under current atmospheric CO_2 concentrations, a number of studies have shown that it is not always true (Maroco *et al.* 1999, Ziska *et al.* 1999, Wand *et al.* 1999, Ghannoum *et al.* 2000, Cousins *et al.* 2002). The increase in rates of net photosynthesis in C_4 species could result in biomass increment under atmospheric CO_2 enrichment.

The second mechanism is the reduction in stomatal conductance that, in turn, leads to a decrease in transpirational water loss. Hence, elevated CO_2 exposure tends to enhance soil moisture conservation, which can improve overall plant water relations and facilitate greater biomass production (Ghannoum *et al.* 2000). Another aspect of the exposure to elevated CO_2 regards the regulation of photochemistry. It is less acknowledged how photochemistry can be regulated at different irradiance regimes under high CO_2 concentration. High irradiances increase the potential for photoinhibition, a process that can be reversible, playing a protective role for the photosynthetic systems, but also irreversible causing serious damages at the photosynthetic apparatus (Alves *et al.* 2002). It has been demonstrated for C_3 plants that the exposure at elevated CO_2 and high light reduces the susceptibility of photosynthetic apparatus to photoinhibition by an enhancement of photosynthetic carbon reduction cycle and the electron flow that drives it (Habash *et al.* 1995, Hogan *et al.* 1997, Griffin *et al.* 2000, Hymus *et al.* 2001). Thus if the exposure of C_4 plants to high CO_2 produces an increase of electron transport flow toward C fixation, it is likely that the exposure to elevated CO_2 could result also in C_4 plants in a beneficial effects in mitigating photoinibitory damage risks at elevated irradiances. However this predicted increase in electron transport may not be observed if growth in elevated pCO_2 results in acclimation of photosynthetic apparatus (Osborne *et al.* 1997, Hymus *et al.* 2001).

Based on the observation in literature that light intensity may alter the response of photosynthetic apparatus of plants at elevated CO_2 and that the growth for long time in elevated CO_2 leads to an acclimation of photosynthesis that may offset the positive effect of the enhanced CO_2 concentration, in this study we aimed to assess how and if light intensity can modify gas exchange and photochemistry at elevated CO_2 in absence of acclimation.

For this purpose two different light intensities (moderate and high) were considered in combination with short-term exposure of 4 h to elevated CO_2. The high light intensity was selected in order to test if the exposure to CO_2 may result in an enhancement of electron flow to photosynthesis and hence in photoprotection of photosynthetic apparatus at high irradiance. In addition, we consider also the importance to test the effect of moderate irradiance in combination to elevated CO_2 because along canopy profile maize leaves receive light varying from high to low intensity throughout the day that likely influences the photosynthetic gain at elevated CO_2.

Materials and methods

Plant material: Seeds of *Zea mays* L. cultivar 121C-D8 were imbibed on rinsed blotting paper with 2 mM $CaCl_2$ and germinated in the dark in a small glass container. The germinated seeds were placed at 1–2 cm depth in 15 l pot filled with a mixture of 30:70 peat/garden soil. The plants were grown outdoors, at the Botanical Garden (Department of Biological Sciences) of Naples University, from late May to July 2003. During this period, plants were irrigated daily and fertilised once a week with a commercial nutritional solution (*Reckitt & Colman*, Italy; N:P:K 20:20:20 + micronutrients). In July, the five topmost fully-expanded leaves of five plants at the vegetative stage (about two meters tall, about 60 day after sowing) were selected for the gas-exchange and chlorophyll *a* fluorescence measurements. The measurements were conducted in the morning on the middle portion of the leaf lamina. The mean irradiance experienced by plants outdoor, in the time of measurement, ranging from 800 $\mu mol\ m^{-2}\ s^{-1}$ in the early morning to 1,800 $\mu mol\ m^{-2}\ s^{-1}$ around midday. During maize plants growth, the monthly mean air temperature ranged between 21ºC in May and 26ºC in July, whereas the monthly mean relative humidity was between 54% in May and 57% in July.

Gas-exchange and fluorescence measurements: Gas-exchange and photochemistry (chlorophyll *a* fluorescence) measurements were performed simultaneously by a portable gas-exchange system (*HCM-1000*, *Walz*, Effeltrich, Germany) in a climatized cuvette equipped with a fiber optic connected with a portable pulse amplitude modulated fluorometer (*MINI-PAM*, *Walz*, Effeltrich, Germany). The fiber optic was inserted at 60° angle at the leaf plane in the cuvette lid to avoid sample darkening.

P_N, g_s, transpiration rate (E), intercellular (C_i) and ambient CO_2 concentration (C_a) were calculated by the software operating in *HCM-1000* using the von Caemmerer and Farquhar equations (1981).

On 30 min dark-adapted leaves, the minimal fluorescence of dark-adapted state (F_0) was induced by light of about 0.5 μmol m^{-2} s^{-1} at the frequency of 0.6 kHz. Then, the maximal fluorescence of dark-adapted state (F_m) was measured at the frequency of 20 kHz by a 1-s saturating light pulse of 8,000 μmol m^{-2} s^{-1}. The saturating pulse intensity was chosen in order to saturate the fluorescence yield but avoiding photoinhibition during the pulse. The steady-state fluorescence level under light, F, was obtained setting light measure at frequency of 20 kHz while the maximal fluorescence level in light-adapted state (F_m') was measured by a 1-s saturating flash of 8,000 μmol m^{-2} s^{-1}. During the measurements in the light, the irradiance of 1,000 and 1,900 μmol m^{-2} s^{-1} was provided by an external light source (*1050-H*, *Walz*, Effeltrich, Germany) positioned on the cuvette plane.

The effective quantum yield of PSII photochemistry (Φ_{PSII}) was expressed according to Genty *et al.* (1989) as $\Phi_{PSII} = (F_m' - F)/F_m'$.

Photochemical quenching was expressed as $q_p = (F_m' - F)/(F_m' - F_0')$. The minimal fluorescence of light-adapted samples (F_0') was determined at 0.6 kHz after turning off the actinic radiation and recording the lowest values of F.

Stern-Volmer nonphotochemical quenching was expressed as $NPQ = (F_m - F_m')/F_m'$ (Bilger and Björkman 1990); the maximum fluorescence (F_m) measured in dark-adapted control leaves was used for the NPQ calculation after each treatments.

***P_N* response curves to *C_i* and short-term treatments**: P_N/C_i response curves were performed at two light intensities: control light and high light in order to determine the level of CO_2 at which P_N saturation occurred under different light intensities. The curves were carried out at 25°C and 65% RH, on five attached and fully expanded leaves of *Zea mays* L. at PPFD of 1,000 μmol m^{-2} s^{-1} for control light and at PPFD of 1,900 μmol m^{-2} s^{-1} for high light.

The control light and high light intensities were obtained by means of artificial light provided by an external light source (*1050-H, Walz*, Effeltrich, Germany) positioned on the cuvette plane of the gas-exchange system.

The different CO_2 concentrations were obtained by a gas-mixing unit (*GMA-4, Walz*, Effeltrich, Germany). In order to generate P_N/C_i curves, the C_a concentrations used were: 1,000; 800, 600, 400, 200, 100, 70, 50, and 40 μmol mol^{-1} (Long and Bernacchi 2003). Photosynthesis was first measured at ambient CO_2 concentration of 400 μmol mol^{-1}, then C_a was lowered stepwise to 200, 100, 50, 40, and 4 μmol mol^{-1}, and P_N was recorded at each level. After completing the measurements at 4 μmol mol^{-1}, C_a was returned to 400 μmol mol^{-1} and P_N was measured again for validation. Once this was achieved, C_a was increased stepwise to 600, 800, and 1,000 μmol mol^{-1}.

The short-term treatment to elevated CO_2 was carried out at control and high light. For measurements to control light, a first leaf group was exposed to CO_2 concentration of 400 μmol mol^{-1} (control CO_2) for 10 min adequate to obtain the P_N steady-state (control) and subsequently to 800 μmol mol^{-1} (elevated CO_2) for 4 h. The measurements at high light were performed on a second leaf group following the same procedure. Leaves from 5 different plants were selected for measurements. Before the short-term exposure to elevated CO_2, maize leaves were initially darkened for 30 min at 25°C and relative humidity of 65% in order to measure the maximum PSII photochemical efficiency (F_v/F_m) at control CO_2. Thereafter, leaves were exposed for 4 h either at control light or high light, 25°C and relative humidity of 65% in an atmosphere containing 800 μmol(CO_2) mol^{-1} and 21% O_2 and the following parameters were determined: P_N, g_s, E, WUE, C_i/C_a, Φ_{PSII}, q_p and NPQ.

Statistical analysis: A paired *t*-test was used to assess the significance of the differences between the two irradiance levels for P_N/C_i and Φ_{PSII}/C_i curves at control CO_2 and high CO_2. Three plants were used, one leaf per plants, for a total of three measurements. The effects of irradiance level (control light, high light) and CO_2 concentration on gas exchange and photochemical parameters during the short-term treatment were assessed using two-way *ANOVA* combined with appropriate post hoc comparison tests (pairwise *Student–Newman–Keuls* test). We used five different plants, one leaf per plant, for a total of five measurements for each parameter. Computations were made with *Sigma-Stat 3.5* software and graphical displays with *SigmaPlot 11.0* software (*Jandel Scientific*, USA).

Results

P_N* and Φ_{PSII} response curves to *C_i: P_N measured at 1,900 PPFD (high light) was statistically higher ($p<0.001$) compared to 1,000 PPFD (control light) starting from 50 μmol mol^{-1} C_i and was saturated at lower C_i values ($p<0.05$) than control light (Fig. 1*A*). P_N decreased significantly after the saturation in control but not in high light. Under high light, Φ_{PSII} was lower ($p<0.001$) compared to control light but, at both irradiances, the Φ_{PSII} activity saturated at ambient C_a concentration and no decrease in Φ_{PSII} values at elevated CO_2 was detected (Fig. 1*B*).

Short-term exposure to elevated CO_2: P_N measured at control light of 1,000 PPFD and elevated CO_2 concentration was statistically lower ($p<0.001$) compared to values at control CO_2 (Fig. 2*A*). On the contrary,

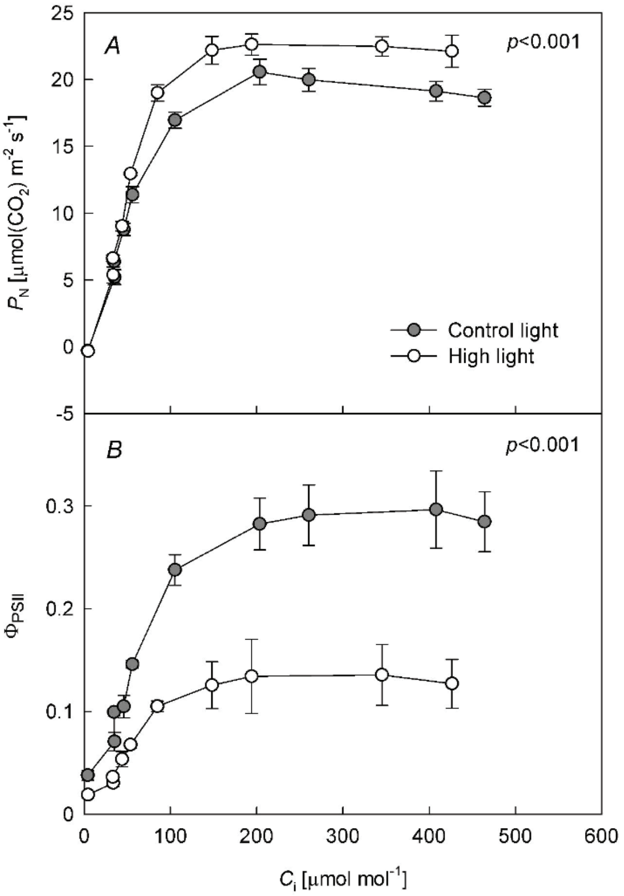

Fig. 1. Net photosynthetic rate (P_N) and effective quantum yield of PSII photochemistry (Φ_{PSII}) response curves to intercellular CO_2 concentration (C_i) at control light of 1,000 μmol m^{-2} s^{-1} (●) and high light of 1,900 (○) μmol m^{-2} s^{-1}. Values are means ± SD ($n = 3$).

at high light of 1,900 μmol m^{-2} s^{-1}PPFD, P_N measured at elevated CO_2 increased compared to control CO_2, although the increment was not significant. At elevated CO_2, P_N was higher ($p<0.001$) under high light than control light.

After the short-term exposure at elevated CO_2, g_s as well as E were lower ($p<0.01$) compared to ambient CO_2 at both light intensities (Fig. 2*B,C*). Between the two irradiance levels no significant difference was detected for g_s, whereas E showed a significant increase ($p<0.01$) only at control CO_2. At elevated CO_2, WUE increased ($p<0.05$) compared to control CO_2, at both control and high light (Fig. 2*D*). No difference in WUE was found between irradiance levels, irrespective of CO_2 treatments. The C_i/C_a ratio was higher under high CO_2 ($p<0.01$) as compared to control CO_2 only at control light, whereas remained unchanged at high light (Fig. 2*E*). At control CO_2 concentration, no difference in C_i/C_a ratio was detected between irradiance levels (Table 1).

The measures of photochemistry showed that Φ_{PSII} was higher ($p<0.001$) under control light compared to high light, but was not affected by exposure to elevated CO_2 (Fig. 2*F*). q_p and NPQ remained unaffected by CO_2 treatments under control light as well as under high light (Fig. 2*G,H*). At both control and high CO_2, q_p was higher and NPQ lower ($p<0.001$) in leaves exposed to control light compared to high light (Table 1).

The results of the two-way *ANOVA* evidence that the interaction between irradiance levels and CO_2 concentrations was significant only for net photosynthetic rate. For photochemistry, differences between irradiance levels were significant for all investigated parameters, whilst no difference occurred between CO_2 concentrations; no interaction was found between irradiance level and CO_2 concentrations (Table 1).

Discussion

In our experiment, in order to detect a possible positive effect of the enhanced CO_2 concentration on photosynthetic apparatus, we avoided the acclimation at elevated CO_2 by means of short-term exposures. The short-term treatment of maize cv. 121C-D8 to elevated CO_2 determined a different behaviour in CO_2 fixation compared to photochemistry in response to light treatments. In agreement with results found by other authors in well watered maize plants exposed to high CO_2 (Samarakoon and Gifford 1996, Ziska and Bunce 1997, Leakey *et al.* 2006, Kim *et al.* 2007) we observed the absence of a significant stimulation of P_N and no variation in C_i/C_a ratio at elevated CO_2 concentration under high irradiance compared to control CO_2. On the contrary, under control light leaves exposed to elevated CO_2 showed a significant reduction in P_N and an increase of C_i/C_a ratio compared to control CO_2, suggesting a limiting effect of elevated CO_2 on photosynthesis at sub-optimal irradiance level at least under short-term exposure. This hypothesis is corroborated by the profile of P_N/C_i response curve: the P_N/C_i curve in C_4 plants is characterized by a steep initial slope and saturation at relatively low C_i. Under high light the saturation of curve depends on the Rubisco activity, whereas under low light it depends on the capacity to regenerate phospho*enol*-pyruvate (PEP) and/or ribulose-1,5-bisphosphate (RuBP) and consequently on the photosynthetic electron transport activity (Berry and Farquhar 1978, von Caemmerer and Farquhar 1999). During short-term exposures at elevated CO_2, at both control and high irradiance, we used irradiances above the region of P_N/PPFD curve in which P_N of maize cv. 121C-D8 is limited by photosynthetic electron transport (D'Ambrosio *et al.* 2003). It has been observed that in C_3 plants the P_N reduction at elevated CO_2 is due to RuBP carboxylation limitation and/or RuBP regeneration limitation (Jacob *et al.* 1995, Rogers and Humphries 2000, Chen *et al.* 2005, Urban *et al.* 2003, Pérez *et al.* 2007). Zhang *et al.* (2009) showed that

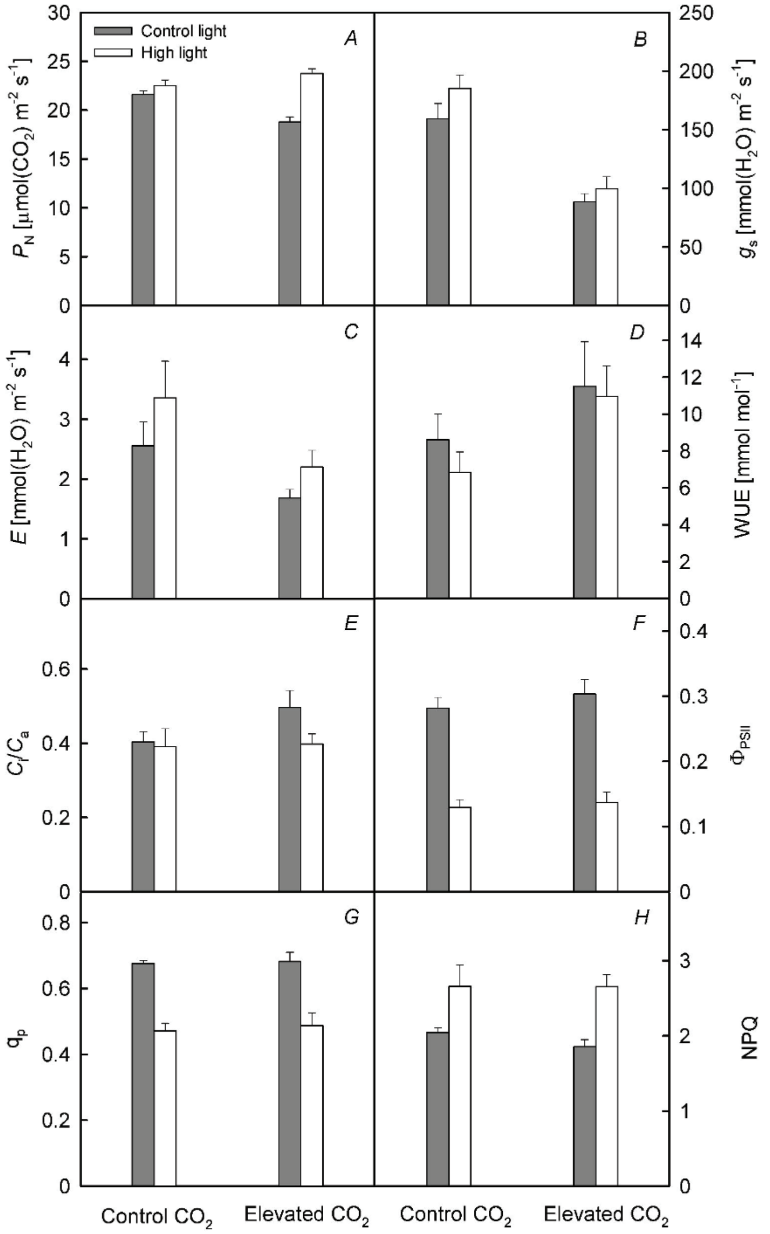

Fig. 2. *A*: net photosynthetic rate (P_N), *B*: stomatal conductance to water (g_s), *C*: transpiration rate (*E*), *D*: water-use efficiency (WUE), *E*: C_i/C_a ratio, *F*: effective quantum yield of PSII photochemistry (Φ_{PSII}), *G*: photochemical quenching (q_p), and *H*: nonphotochemical quenching (NPQ) at light of 1,000 (■) and 1,900 (□) μmol m^{-2} s^{-1}, under control CO_2 and elevated CO_2 concentration after 4 h of short-term exposure. Values are means ± SD (n = 5).

in wheat the P_N reduction at elevated CO_2 is largely attributed to RuBP carboxylation limitation without RuBP regeneration limitation. But here, as Φ_{PSII} did not decrease during the short-term exposure to elevated CO_2, we exclude that P_N reduction at elevated CO_2 and moderate light was due to a limitation in PEP and/or RuBP regeneration, because the resulting electron transport activity was not limiting for substrate replacement (von Caemmerer and Farquhar 1999).

In our view, the higher C_i/C_a ratio at elevated CO_2/control light, as compared to control CO_2/control light, denotes a limited mesophyll capacity to CO_2 fixation likely due to a reduced PEPC activity when plants are exposed to moderate irradiances and elevated CO_2 concentrations. The higher level of CO_2 within the cell might determine a decline in intracellular pH (Bown 1985, Siriphanich and Kader 1986). It is well known that any perturbation of intracellular pH influences the activity of many enzymes. PEPC activity is regulated by cytosolic pH and by light level (Bonugli and Davies 1977, Bassi and Passera 1982). The exposure to control light and elevated CO_2 might determine limitation in PEPC activity due both to inadequate light level and high CO_2 concentration leading to the rise in intercellular CO_2 concentration. At elevated CO_2 and high light we did not observe a decline in photosynthesis and a rise C_i/C_a ratio probably because the exposure to high light stimulates the PEPC activation favouring the intracellular CO_2 uptake by photosynthesis (Bassi and Passera 1982).

Table 1. Levels of significance (*P* values) from the two-way *ANOVA* for comparison between irradiance level (control light: 1,000 μmol m^{-2} s^{-1}; high light: 1,900 μmol m^{-2} s^{-1}) and for comparison between [CO_2]: control CO_2 – 400 μmol(CO_2) mol^{-1}; high CO_2 – 800 μmol(CO_2) mol^{-1}]. Notes: Terms for *ANOVA* model (degree of freedom in parenthesis) are: irradiance level (1), CO_2 concentrations (1), irradiance level × CO_2 concentrations (1), residual (16), total (19). Pairwise multiple comparison by *Student-Newman-Keuls* method. P_N – net photosynthetic rate; g_s – water stomatal conductance; *E* – transpiration rate; WUE – water-use efficiency; C_i/C_a – ratio of intercellular to ambient CO_2 concentration; Φ_{PSII} – effective quantum yield of PSII photochemistry; q_p – photochemical quenching; NPQ – nonphotochemical quenching. *Bold values* represent a statistically significant difference between conditions.

Variable	Irradiance level	[CO_2]	Irradiance level × [CO_2]	Post hoc comparison tests			
				between irradiance level		between CO_2 concentration	
				AC	EC	ML	HL
P_N	**<0.001**	0.134	**<0.001**	0.213	**<0.001**	**0.001**	0.095
g_s	0.102	**<0.001**	0.494	0.104	0.474	**<0.001**	**<0.001**
E	**0.003**	**<0.001**	0.463	**0.009**	0.073	**0.005**	**<0.001**
WUE	0.153	**<0.001**	0.437	0.124	0.626	**0.017**	**0.002**
C_i/C_a	**0.032**	0.113	**0.051**	0.758	**0.016**	**0.006**	0.878
Φ_{PSII}	**<0.001**	0.070	0.386	**<0.001**	**<0.001**	0.063	0.468
q_p	**<0.001**	0.356	0.659	**<0.001**	**<0.001**	0.728	0.337
NPQ	**<0.001**	0.238	0.249	**<0.001**	**<0.001**	0.106	0.985

Our results indicate light level as an important factor in determining the photosynthetic response of *Z. mays* to short-term exposure at elevated CO_2. This aspect could be considered in models that simulate the C_4 response to high CO_2 since light conditions and shading within the canopy change significantly (Larcher 2003).

The exposure to elevated CO_2 induced at both control- and high light an increase in WUE as a consequence of leaf transpiration decrease. The reduced leaf transpiration is responsible for the preservation of water status of the whole plant under atmospheric CO_2 enrichment and for the conservation of soil water content (Leakey *et al.* 2006).

This aspect may reveal important in a future scenario of climate change where a reduction in precipitation is expected (IPCC 2007). However it has also to be considered that an increase in instant WUE (P_N/g_s) does not necessarily result in an increase in integrated WUE (biomass increment/transpiration), as a decline in transpiration can lead to a decrease in growth.

Although at control light the short-term exposure to elevated CO_2 determined a reduction of P_N, Φ_{PSII} remained fairly constant as compared to ambient CO_2. We suggest that at high light the reductive power was used mainly in photosynthetic carbon reduction cycle, while at control light, as the electron transport was not down-regulated by carbon metabolism, it was utilized in sinks other than carbon assimilation process. For instance, it has been demonstrated that Mehler reaction has a fundamental role in maize exposed at low temperature (Massacci *et al.* 1995, Fryer *et al.* 1998) and high light (D'Ambrosio *et al.* 2003). Also C_4 acid over cycling due to CO_2 leakage from bundle sheath to mesophyll cells represents a very active process in consuming electrons (Furbank *et al.* 1990, Henderson *et al.* 1992), as well as photorespiration under water stress (Lal and Edwards 1996, Martinelli *et al.* 2007) and in old leaves (Dai *et al.* 1995, Kiirats *et al.* 2002).

In our opinion, we exclude that the slight increase of Φ_{PSII} observed at control light under elevated CO_2 could be attributable to the over cycling, since the exposure to elevated CO_2 could compensate the CO_2 leakage from bundle sheath to mesophyll cells. On the contrary, the possible reduction in PEPC activity could expose Rubisco to ambient O_2 determining an increase of photorespiration and, in turn, a reduction of photosynthetic rate. As a consequence of the increase of electron utilization in alternative sinks, the fraction of PSII open reaction centres (q_P) remained fairly constant in elevated CO_2 compared to control CO_2 leaves evidencing the positive contribution of these processes in preventing photoinhibition. Irrespective of CO_2 concentration, the exposure to high light determines a reduction of photochemistry and a rise in NPQ compared to control light, indicating that, in this context, thermal dissipation plays a main role in preventing photodamages. The importance of thermal dissipation as safety mechanism is consistent with q_P values that are maintained under the threshold of photoinhibitory damage (Chow 1994).

Our results indicated that both control and high light in combination with elevated CO_2 did not result in a stimulatory effect on photosynthesis and the effective quantum yield of PSII photochemistry. More specifically, the exposure at moderate light under high CO_2 induced a decrease in CO_2 fixation but not in photochemistry, suggesting that the low photosynthetic rate was due to limitation in photosynthetic dark reaction rather than in PSII electron transport activity. High light together with high CO_2 exposure did not produce an increase of electron transport flow toward C fixation, thus the exposure to elevated CO_2 did not result in a beneficial effects in mitigating photoinibitory damage risks at elevated irradiances. However, despite no advantage on photosynthetic carbon gain, a decrease in transpirational water loss was achieved under high CO_2, at both irradiances, resulting in improving of plant water relations. The different response of maize photosynthetic apparatus to light regime under high CO_2 has to be considered in models that simulate the maize response to CO_2 rising as the changes in light intensity within the canopy could represent an important factor in influencing the photosynthetic gain at elevated CO_2.

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