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Different relationship between electron transport and CO_2 assimilation in two *Zea mays* cultivars as influenced by increasing irradiance

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Abstract

Gas exchange and fluorescence parameters were measured simultaneously in two *Zea mays* L. cultivars (Liri and 121C D8) to assess the relationship between the quantum yield of electron transport (Φ_{PS2}) and the quantum yield of CO_2 assimilation (Φ_{CO2}) in response to photosynthetic photon flux density (PPFD). The cv. Liri was grown under controlled environmental conditions in a climate chamber (CC) while cv. 121C D8 was grown in CC as well as outdoors (OT). By exposing the two maize cultivars grown in CC to an increasing PPFD, higher photosynthetic and photochemical rates were evidenced in cv. Liri than in cv. 121C D8. In Liri plants the Φ_{PS2}/Φ_{CO2} ratio increased progressively up to 27 with increasing PPFD. This suggests that the reductive power was more utilised in non-assimilatory processes than in CO_2 assimilation at high PPFD. On the contrary, by exposing 121C D8 plants to increasing PPFD, Φ_{PS2}/Φ_{CO2} was fairly constant (around 11–13), indicating that the electron transport rate was tightly down regulated by CO_2 assimilation. Although no significant differences were found between Φ_{PS2}/Φ_{CO2} of the 121C D8 maize grown under CC and OT by exposing them to high PPFD, the photosynthetic rate and photochemical rates were higher in OT maize plants.

Additional key words: chlorophyll fluorescence; maize; net photosynthetic rate; photochemistry; stomatal conductance.

Introduction

Any limitation of CO_2 assimilation may increase the imbalance between the absorbed photons and the amount of them utilised in photochemistry. The photon flux absorbed in excess may reduce the photosynthetic efficiency through photoinactivation of photosystem (PS) 2, commonly called photoinhibition (Kok 1956, Powles 1984, Long *et al.* 1994). The use of absorbed photons in photochemistry is a mechanism disposing safely of photon energy excess, avoiding an over-reduction of electron transport, and photo-protecting PS2 (Osmond and Grace 1995).

The relationship between the quantum yield of electron transport (Φ_{PS2}) and the quantum yield of CO_2 fixation (Φ_{CO2}) depends on the partitioning of reductants between CO_2 assimilation and non-assimilatory sinks (Genty *et al.* 1989, Edwards and Baker 1993). Several processes may sustain the non-assimilatory electron transport: photorespiratory carbon oxidation, oxygen reduction by Mehler ascorbate peroxidase pathway, ferredoxin-dependent reduction of monodehydroascorbate, chlororespiration, nitrate and sulphate reduction, fatty acid biosynthesis, NADPH-dependent reduction of oxaloacetate to malate, and cyclic electron flow around the PS1 (Heber *et al.* 1978, Furbank and Horton 1987,

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Abbreviations: C_i – intercellular CO_2 concentration; C_i/C_a – ratio of intercellular to ambient CO_2 concentration; CC – climate chamber; Chl – chlorophyll; F_m – maximal fluorescence when all PS2 reaction centres are closed in the dark-adapted state; F_m' – maximal fluorescence when all PS2 reaction centres are closed in the light-adapted state; F_0 – minimal fluorescence when all PS2 reaction centres are open in the dark-adapted state; F_0' – minimal fluorescence when all PS2 reaction centres are open in the light-adapted state; F_v/F_m – photochemical efficiency of PS2 in the dark-adapted state; g_s – stomatal conductance; NPQ – non-photochemical quenching; OT – outdoors; P_N – net photosynthetic rate; P_{Nsat} – irradiance saturated net photosynthetic rate; PPFD – photosynthetic photon flux density; PS – photosystem; Γ – CO_2 compensation point; Φ_{CO2} – quantum yield of CO_2 assimilation; Φ_{PS2} – quantum yield of electron transport; Φ_{PS2}/Φ_{CO2} – ratio between the quantum yield of electron transport and the quantum yield of CO_2 assimilation.

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Scheibe 1987, Edwards and Baker 1993, Osmond and Grace 1995, Asada 1999, Niyogi 1999, Nixon 2000). The parameter defining the relationship between electron transport and CO_2 fixation is the Φ_{PS2}/Φ_{CO2} ratio. This ratio in *Zea mays* is constant within the range of 11–13 for a wide variety of environmental conditions (irradiance, CO_2 concentration, temperature) (Genty *et al.* 1989, Krall and Edwards 1991, Krall *et al.* 1991, 1992, Edwards and Baker 1993, Siebke *et al.* 1997). Alternative electron acceptors act as sinks removing excess of absorbed photon energy and preventing over-reduction of the electron transport giving photoprotection by phytochemistry (Niyogi 1999). However, a major utilisation of reductants in sinks other than CO_2 fixation was found in maize grown at low temperatures (Fryer *et al.* 1995, Massacci *et al.* 1995) and in drought-stressed leaves of sweet sorghum (Massacci *et al.* 1996). A chill-induced reduction of photosynthesis in maize is associated with an increase in Φ_{PS2}/Φ_{CO2}, implying a greater allocation of electron transport rate to non-assimilatory sinks (Fryer *et al.* 1998). Little attention has been given to the assessment of Φ_{PS2}/Φ_{CO2} in maize exposed to increasing PPFD.

The aim of this work was to examine the Φ_{PS2}/Φ_{CO2} ratio in response to PPFD. Measurements of net CO_2 exchange (P_N) were performed simultaneously to those of chlorophyll (Chl) fluorescence emission in *Zea mays* plants grown under controlled environmental conditions (CC) and outdoors (OT).

Materials and methods

Plants: Seeds of two *Zea mays* L. cultivars (Liri and 121C D8) were imbibed on blotting paper rinsed with 2 mM $CaCl_2$ and germinated in the dark in a small glass container. Seeds of cv. Liri were obtained from *Plant Seeds Exchange Office of F.A.O.,* Rome, Italy, while seeds of 121C D8 were supplied by *Maize Genetics Cooperation-Stock Center*, University of Illinois, Urbana, USA. The germinated seeds were placed 1–2 cm deep in pots of 30 cm diameter (15 000 cm^3) filled with 1 : 1 peat/soil.

Growth conditions: Cv. 121C D8 plants were grown OT and in CC from April to July 1999, while cv. Liri plants were grown in CC only. Plants in CC were exposed to a photoperiod of 15 h, day/night temperatures of 25/15 °C, a relative humidity of 60/85 % (day/night), and PPFD of 280 $\mu mol\ m^{-2}\ s^{-1}$. Irradiation was provided by a series of 58 W fluorescent tubes (*Philips TLD 54* and *84*) and halogen lamps (*Philips HPI-T* 400 W). PPFD was measured with a quantum sensor (*Li-Cor 185*, *Li-Cor*, Lincoln, NE, USA). The OT maize plants were situated in the open area on a terrace exposed east-south-west. To avoid rainfall without shading the plants, a plastic shed protected this area. Plants were watered daily to compensate for the water loss due to transpiration and fertilised once a week with a commercial nutritional solution (*Gesal Tecno-Pro*; N : P : K 20 : 20 : 20 + trace elements of Mg, B, Cu, Fe, Mn, Zn, and Mo) at a rate of 2 kg m^{-3}. The environmental conditions experienced by OT plants during growth are reported in Fig. 1. During the early development of plants the minimum night temperature was frequently below 15 °C while the maximum day temperature never exceeded 26.8 °C. During the hottest period the minimum night temperature was 18 °C while the maximum day temperature was 32–34 °C.

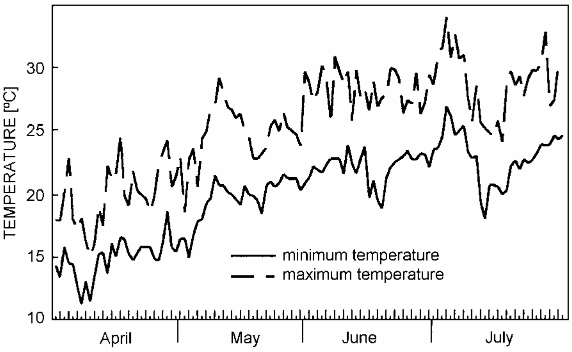

Fig. 1. Maximum and minimum air temperatures in Naples during the period April-July 1999.

Gas exchange was measured by an open gas exchange system (Minicuvette System, *Walz*, Effeltrich, Germany) equipped with an infrared gas analyser (*UNOR*, *Maihak*, Hamburg, Germany). To avoid water vapour interference on differential CO_2 analyser, reference and sample gases were dried to 0 °C dew-point by passing the gases through ice traps. A special climatised cuvette (*GK-022*, *Walz*, Effeltrich, Germany) was used to fit the fibre optic of fluorometer at 60 °C to the leaf plane. Cuvette temperature was set at 25 °C and leaf temperature was measured with a thermocouple on the underside of the leaf. The air stream was humidified by bubbling through water at ambient temperature. The relative humidity of the air stream was fixed at 65 % by means of a water-condensing system (cold trap *KF*, *Walz*, Effeltrich, Germany) installed after the humidifying system and kept constant in the cuvette by an electronic controlled water-trapping system. The humidity of the air entering and leaving the leaf cuvette was measured by two dew point mirror hygrometers (*MTS-MK1*, *Walz*, Effeltrich, Germany) linked to the water-trapping system. Any variation of outgoing humidity compared to incoming air at the leaf chamber lets the water-trapping system run. Transpiration rate was determined by measuring the flow of air stream through the water trapping. Actinic irradiation was provided by a halogen lamp (*Osram*, *Xenophot HLX*, 12 V, 75 W) equipped with an IR-filter. The values of steady-state photosynthesis at each PPFD were obtained in a time period of 45–60 min. The leaf area was reproduced with a photocopier and determined based on the mass of the corresponding paper area. The calculation of P_N and stomatal conductance (g_s) was done according to the equations of Caemmerer and Farquhar (1981). In the Liri maize, P_N in CO_2-free air ($C_i = 0$) was also determined at 25 °C, 65 % relative humidity, and PPFD of 1 000 μmol m^{-2} s^{-1}. P_N at $C_i = 0$ is considered an estimate of the sum of photorespiration and mitochondrial respiration in the light (Escalona *et al.* 1999). Then the CO_2 compensation concentration (Γ) was determined by measuring P_N response to low CO_2 concentration (0–4 Pa) and extrapolating C_i at $P_N = 0$ through the CO_2 concentration axis (Ku *et al.* 1991).

Chl *a* fluorescence was measured by a pulse amplitude modulated fluorometer (*PAM-2000*, *Walz*, Effeltrich, Germany) as described by Schreiber *et al.* (1986). The minimal and maximal fluorescence yields (F_0 and F_m) were determined in leaves after 20 min of dark adaptation. The fibre optics of the fluorometer was situated at 60° and at about 7 mm from the sample. The minimal fluorescence (F_0) was excited by a measuring beam of weak irradiance 0.1 μmol m^{-2} s^{-1} from a pulse LED with peak emission at 650 nm. The maximal fluorescence yield of the dark- and light-adapted sample (respectively F_m and F_m') was determined by applying a 1 s saturating "white light" pulse (about 3 000 μmol m^{-2} s^{-1}). The saturating "white light" pulse was chosen to saturate the fluorescence yield but avoiding photoinhibition during the pulse. The quantum yield of PS2 linear electron transport (Φ_{PS2}) was determined during the steady state of photosynthesis according to Genty *et al.* (1989). F_0' (minimal fluorescence yield in the light-adapted sample) was recorded after turning off the actinic radiation and immediately turning on a 3 s far-red radiation to fully re-oxidise the electron transport chain between PS2 and PS1. The measurements of F_0 and F_0' were performed with the measuring beam set at 600 Hz, while the measurements of steady-state fluorescence (F), dark-adapted maximal fluorescence (F_m), and PPFD-adapted maximal fluorescence (F_m') were obtained with the measuring beam automatically switching to 20 kHz. Resolution of non-photochemical quenching (NPQ) was calculated using the saturating pulse at the steady state of photosynthesis. NPQ was calculated as Stern-Volmer quenching ($NPQ = F_m - F_m'/F_m'$) (Bilger and Björkman 1990). As the fluorescence and gas exchange measurements were made simultaneously, all the parameters were recorded at the same actinic irradiance. The calculation of the Chl fluorescence parameters, if not specified, was according to van Kooten and Snel (1990).

Experimental protocol: Measurements were performed on fully developed leaves according to the following experimental protocol. After darkening leaves for about 20 min, the respiration rate, the basic (F_0) and maximal fluorescence (F_m) were determined. From the fluorescence parameters of dark-adapted leaves the F_v/F_m ratio [= $(F_m - F_0)/F_m$] was calculated indicating the photochemical efficiency of PS2. The responses of P_N to various PPFDs were determined at 25 °C and 65 % of relative humidity by exposing leaves progressively to increasing PPFD until saturating irradiance. At each PPFD, when the steady state was reached, P_N was monitored and a saturating radiation pulse was applied in order to measure the quantum yield of linear electron transport. Afterwards the light was switched off and a 3-s far-red radiation was applied to measure the F_0' fluorescence. After an exposure of leaves to the whole range of experimental PPFDs, leaves were again darkened for about 20 min in order to measure the basic and the maximum fluorescence.

Statistical analysis: Data were processed by analysis of variance (*ANOVA*) to test whether the variations in response to different irradiances were significant. The LSD-test (Least Significant Difference) was used to determine existing differences based on a significance level of $p<0.05$. Data are the means ± standard error of at least three measurements. They were analysed with an one-way *ANOVA* by using the statistical package *Statgraf* (version 1.0).

Results

Gas exchange measurements: The curve relating P_N and PPFD of cv. Liri grown in CC was statistically higher ($p<0.001$) over the range 600–1 600 μmol m^{-2} s^{-1} than that of cv. 121C D8 grown in CC or OT (Fig. 2*A*). A significant difference ($p<0.005$) was also found between the PPFD response photosynthetic curve of the 121C D8 maize grown in CC or OT. Liri plants showed a higher photon saturated rate of P_N (P_{Nsat}) [19.4 μmol(CO_2) m^{-2} s^{-1}] than 121C D8 plants grown in CC [13.9 μmol(CO_2) m^2 s^{-1}] or OT [17.7 μmol(CO_2) m^2 s^{-1}]. P_N was saturated at about 1 200 μmol m^{-2} s^{-1} in cv. Liri, but already at 600 μmol m^{-2} s^{-1} in cv. 121C D8 grown in CC. It did not saturate even at the highest PPFD applied to OT plants of 121C D8 maize (Fig. 2*A*).

g_s increased with PPFD and was significantly higher over the PPFD range of 400–1 600 μmol m^{-2} s^{-1} in Liri plants grown in CC than in CC and OT plants of 121C D8 ($p<0.0001$). Moreover, g_s in OT plants of 121C D8 was significantly higher ($p<0.05$) than in the CC ones (Fig. 2*B*).

The intercellular CO_2 concentration around mesophyll cells was expressed as the ratio of intercellular to ambient CO_2 concentration (C_i/C_a). The C_i/C_a ratio of Liri maize was significantly higher ($p<0.005$) than that of CC and

OT plants of 121C D8 (Fig. 2*C*). On the contrary, no significant difference was found in C_i/C_a between the CC and OT plants of cv. 121C D8.

The CO_2 compensation point (Γ) and P_N at CO_2-free air in cv. Liri were about 22 Pa and –0.31 μmol(CO_2) m^{-2} s^{-1}, respectively.

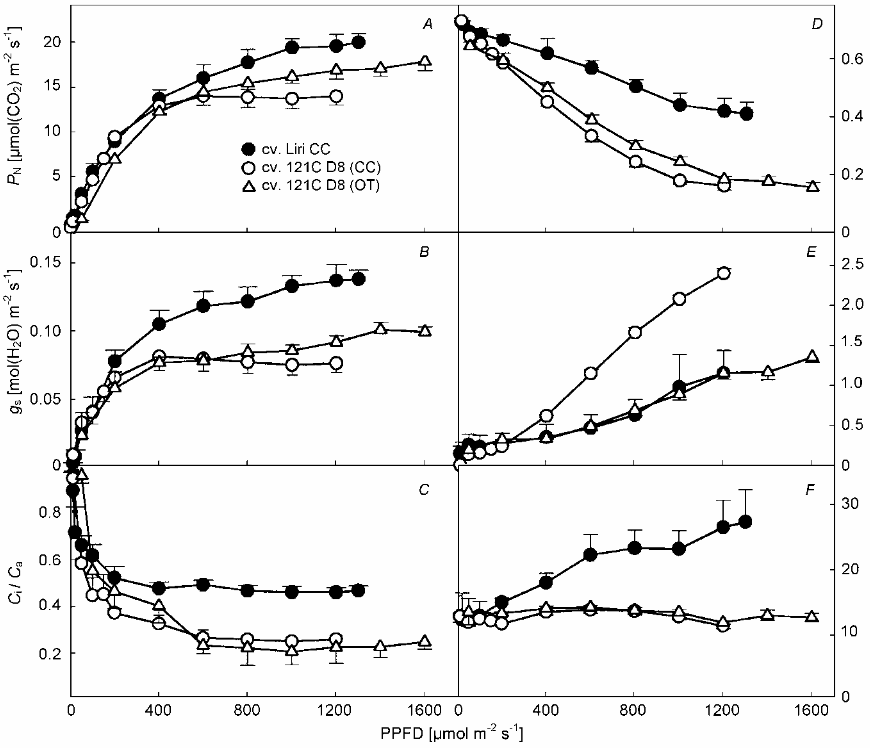

Fig. 2. Net photosynthetic rate, P_N (*A*), stomatal conductance, g_s (*B*), C_i/C_a ratio (*C*), quantum yield of photosystem 2 linear electron transport (Φ_{PS2}) (*D*), thermal dissipation expressed by the non-photochemical quenching coefficient, NPQ (*E*), and the ratio between the quantum yield of electron transport and the quantum yield of CO_2 assimilation (Φ_{PS2}/Φ_{CO2}) (*F*) in response to different photosynthetic photon flux densities, PPFD in *Zea mays* plants of cv. Liri (●), cv. 121C D8 (CC) (○), and cv. 121C D8 (OT) (Δ). Measurements at 25 °C and relative humidity of 65 %. Means ± standard errors of at least three measurements.

Chl *a* fluorescence: The quantum yield of PS2 linear electron transport (Φ_{PS2}) decreased by increasing the PPFD in maize cultivars grown either in CC or OT (Fig. 2*D*). However, the Φ_{PS2} values were significantly higher ($p<0.005$) in Liri than in 121C D8; moreover in the cv. 121C D8 the Φ_{PS2} values were significantly higher ($p<0.005$) in OT than CC plants. The measurements of non-photochemical quenching (NPQ) showed in the range 400–1 200 μmol m^{-2} s^{-1} a significantly higher extent of thermal dissipation in CC plants of 121C D8 maize ($p<0.05$) compared to the OT plants of the same cultivar and to Liri maize (Fig. 2*E*). No significant difference was found between the NPQ values of cv. Liri and of 121C D8 OT plants.

The Φ_{PS2}/Φ_{CO2} ratio showed a different pattern in the two maize genotypes in response to increasing PPFDs (Fig. 2*F*). At low PPFD the Φ_{PS2}/Φ_{CO2} was about 12 in all the plant groups, but by increasing PPFD the ratio reached a value as high as 27 in cv. Liri while it remained fairly constant (about 11–13) in cv. 121C D8 plants grown either in CC or OT.

Discussion

Relationship between electron transport and P_N in response to PPFD: The maize cultivars Liri and 121C D8 grown under the same CC conditions showed a significantly different PPFD response photosynthetic curve over the PPFD range 600–1 200 μmol m^{-2} s^{-1} (Fig. 2*A*). The higher P_N observed in Liri maize was related to the greater g_s (Fig. 2*B*). The highest values of C_i/C_a in cv. Liri were a consequence of the greater g_s compared to cv. 121C D8: in the mesophyll cells of Liri maize the P_N was higher than the carboxylation rate.

The higher P_N of Liri plants was also accompanied by a significantly higher Φ_{PS2} compared to the 121C D8 maize (Fig. 2*D*). The higher rate of photochemistry observed in cv. Liri suggested a different strategy of photochemical regulation than in 121C D8 maize. In cv. Liri the Φ_{PS2}/Φ_{CO2} ratio increased progressively by increasing PPFD (Fig. 2*F*); a high value was already evident when leaves were exposed to a little higher PPFD than that of the growth. Hence, in Liri maize the reductive power was more utilised in non-assimilatory processes than in CO_2 assimilation. The high values of Φ_{PS2}/Φ_{CO2} in cv. Liri evidenced that the photochemical activity was the main way to dissipate safely the excess of excitation energy. In fact, the electron transport rate was never saturated at PPFDs tested in our experiments (data not shown) indicating that other sinks, different from the assimilatory process, were likely to accept these electrons. In this way the energy excitation excess can be dissipated by photochemical activity avoiding the over-reduction of PS2 reaction centres. The main role of photochemistry to dissipate the energy excitation excess was also confirmed by a lower degree of thermal energy dissipation (NPQ) compared to 121C D8 (Fig. 2*E*).

In C_4 plants the absorbed photons may be totally used to drive the CO_2 fixation so the electron transport rate is tightly down-regulated by CO_2 assimilation when no other alternative reductive power sink occurs (Krall and Edwards 1992). In maize cultivars and other C_4 plants the relationship between electron transport rate and carbon fixation, expressed by Φ_{PS2}/Φ_{CO2}, has often been found constant over a wide range of environmental conditions, even in photoinhibited maize leaves (Edwards and Baker 1993). In contrast, our results suggest that in Liri maize the electron transport rate did not match the CO_2 fixation activity at increasing PPFD. Therefore non-assimilatory processes have to act as sinks of reductive power at high PPFDs. Since several studies have reported that photorespiration is not completely suppressed in C_4 plants (Marek and Stewart 1983, de Veau and Burris 1989, Jenkins *et al.* 1989, He and Edwards 1996), Liri maize leaves were also exposed to an atmosphere containing 2 % O_2 to inhibit photorespiration. No significant variations in gas-exchange and fluorescence parameters were observed (data not shown) and, consequently, it was concluded that photorespiration was not a sink for electrons in this maize cultivar. Moreover, Γ and P_N in CO_2-free air (at 1 000 μmol m^{-2} s^{-1}, 25 °C, and relative humidity of 65 %) may estimate the sum of photorespiration and mitochondrial respiration in the light (Escalona *et al.* 1999). The obtained results [$\Gamma = 22$ Pa, P_N in CO_2-free air $= -0.31$ μmol(CO_2) m^{-2} s^{-1}] demonstrated that the photorespiratory rate was not significant. One of the most probable mechanisms to increase the electron flow relative to CO_2 assimilation may be the O_2 reduction *via* the Mehler reaction (Osmond and Grace 1995, Savitch *et al.* 2000). This process plays an important role as a sink of electron acceptors in chill-stressed maize leaves (Massacci *et al.* 1995, Fryer *et al.* 1998). Furbank *et al.* (1983) observed Mehler reaction in mesophyll chloroplasts of C_4 species and proposed a role in the production of extra ATP for the pseudocyclic photophosphorylation. Even if evidence for significant rates in *in vivo* leaves is lacking, Laisk and Edwards (1998) suggested that the Mehler reaction is an important sink for electrons in C_4 plants but they estimated rates too low to account for the extra ATP demand. Our values suggest that O_2 reduction *via* the Mehler reaction might operate in C_4 plants also at high PPFDs providing a safe dissipation of the photon energy absorbed in excess. The O_2 reduction produces reactive oxygen species that are scavenged by detoxification systems (Asada 1999). Even if in this work activities of enzymes involved in the scavenging of reactive oxygen species are not reported, the well documented increased contents of enzymes scavenging the reactive oxygen species can account for the role of O_2 as an additional sink for electrons generated by the photosynthetic electron transport (Massacci *et al.* 1995, Fryer *et al.* 1998).

Another possible electron sink could be the NADPH-dependent reduction of oxaloacetate to malate associated to over-cycling of the C_4-acid cycle relative to the rate of CO_2 assimilation. In order to maintain a high CO_2 concentration in the bundle sheath cells, C_4 plants compensate CO_2 leakage from the bundle sheath to mesophyll cells by over-cycling of the C_4-acid cycle (Hatch 1987, Furbank *et al.* 1990). In mature leaves the C_4-acid cycle can be 25 % faster than the photosynthetic rate (Farquhar 1983, Henderson *et al.* 1992). Over-cycling involves additional energy because ATP is required for phospho*enol*pyruvate synthesis (Furbank *et al.* 1990). Moreover, the reduction of oxaloacetate to malate is a valve to remove excess NADPH acting as an electron sink (Scheibe 1987). According to Furbank *et al.* (1990) a 100 % C_4-acid over-cycling would increase the quantum requirement from 12 to 24 mol(quantum) mol^{-1}(CO_2). However, even if a 100 % C_4-acid over-cycling may occur in Liri maize, the quantum requirement increase would not fully account for the raise of the Φ_{PS2}/Φ_{CO2} ratio up to 27. Although C_4-acid over-cycling may influence the Φ_{PS2}/Φ_{CO2}, it is not responsible for the observed increase of this ratio.

Chlororespiration, the process occurring in the chloroplasts, could be an alternative sink of electron acceptors (Nixon 2000). Electrons are transferred in the chloroplasts from NADPH to O_2 by a respiratory chain through the plastoquinone pool. The discovery of a chlororespiratory plastoquinone oxidase, that removes electrons from the plastoquinone pool to reduce O_2, indicates another pathway by which electrons are transferred from PS2 to O_2. Chlororespiration may be an electron acceptor sink when the photon energy is absorbed in excess (Niyogi 2000). However, we exclude a significant role of chlororespiration in Liri maize exposed to increasing PPFD because this pathway is only 0.3 % of the overall photon-saturated electron transport (Field *et al.* 1998, Ort and Baker 2000).

In cv. 121C D8 the Φ_{PS2}/Φ_{CO2} ratio was fairly constant (within the range of 11–13) and the data agree with those of other studies (Massacci *et al.* 1995, Ghannoum *et al.* 1998). This means that in 121C D8 maize the electron transport was tightly down regulated by carbon metabolism and no alternative electron sink occurred. Therefore partitioning of reductive power between CO_2 assimilation and non-assimilatory processes did not change in response to PPFD. In cv. 121C D8 the photochemical activity did not contribute to dissipating the excess of excitation energy as observed in cv. Liri. Even if in CC plants of cv. 121C D8 the activity of photochemistry was significantly lower than in the cv. Liri, a higher thermal energy dissipation (NPQ) might contribute to dissipating the excess of energy.

Evidence that two different strategies have been adopted to dissipate at the same extent, the excitation energy excess in PS2 comes in the studied maize cultivars from F_v/F_m that indicates the photochemical efficiency of PS2. The F_v/F_m ratio measured in both Liri and 121C D8 cultivars after exposure to progressively increasing PPFD showed almost the same significant decrease of about 10 % of the starting value ($p<0.05$) (Table 1).

Table 1. Photochemical efficiency of photosystem 2 in *Zea mays* plants expressed as the F_v/F_m ratio. Measurements were carried out in cv. Liri, grown in a climate chamber, as well as in cv. 121C D8 maize, grown outdoors (OT) and in a climate chamber (CC), before and after exposure to progressively increasing photosynthetic photon flux density (PPFD). F_v/F_m values as a percentage of the control value measured before exposition to progressively increasing PPFD are in brackets. Means ± standard error of at least three measurements.

Cultivar	F_v/F_m before irradiation	after irradiation
Liri	0.7680 ± 0.0038 (100)	0.7010 ± 0.0206 (91.3)
121C D8 (CC)	0.7530 ± 0.0035 (100)	0.6660 ± 0.0100 (88.4)
121C D8 (OT)	0.7200 ± 0.0177 (100)	0.6580 ± 0.0141 (91.5)

Comparison of the 121C D8 plants grown in CC with the OT-grown ones showed that different growth environment of 121C D8 plants influenced both P_N and photochemical activity (Fig. 2*A,D*). The relationship between the electron transport and the CO_2 assimilation (Φ_{PS2}/Φ_{CO2}) was constant in response to PPFD suggesting that the electron transport was tightly down-regulated by carbon metabolism in both conditions (Fig. 2*F*). However, the CC maize plants showed a significantly higher thermal dissipation than the OT plants (Fig. 2*E*). The CC maize plants were grown at a low PPFD and therefore they were exposed to a more severe irradiance stress than the OT plants that might have already experienced temporarily high irradiances during the day.

In the 121C D8 maize grown in CC the higher thermal dissipation than in the OT maize was able to keep the photochemical efficiency of PS2 similar to that observed in OT maize (Table 1). In fact, in 121C D8 plants grown both in CC and OT conditions the same significant decrease (about 10 % of the starting value) ($p<0.05$) of F_v/F_m was observed after the PPFD response photosynthetic curves, regardless of the different environmental growth conditions.

In conclusion, we found a different relationship between electron transport and CO_2 assimilation in two different maize cultivars. In cv. Liri the electron transport rate did not match the CO_2 fixation activity by increasing the PPFD and therefore non-assimilatory processes had to act as sinks of reductive power at high PPFD. On the contrary, in cv. 121C D8 maize the relationship between electron transport and CO_2 assimilation was constant, regardless of the different growth environment.

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